EDAPHIC ECOLOGY OF *FESTUCA NOVAE-ZELANDIAE*, *LOTUS PEDUNCULATUS* AND *TRIFOLIUM REPENS* ON CRAIGIEBURN HIGH COUNTRY YELLOW-BROWN EARTH & RELATED SOILS

A thesis

Submitted in partial fulfilment

of the requirements for the degree

of

Doctor of Philosophy

in the

University of Canterbury

by

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Lincoln College

1987

Frontispiece: The Cave Stream terrace sequence, Craigieburn Study Site

ABSTRACT

Fescue tussock (*Festuca novae-zelandiae*) dominates the physiognomy of the largest indigenous grassland association in New Zealand. Little is known regarding the population biology and edaphic ecology of the tussock. For pastoral development of fescue tussock grasslands evaluation of the legumes lotus *(Lotus pedunculatus* cv 'Maku') and white clover (*Trifolium repens* cv 'Huia') is required. The aim of this study was to investigate the role of edaphic factors, principally mineral nutrition, in these plants.

To investigate a range of soils representative of those occurring widely throughout the South Island montane tussock grasslands, two soil development sequences were studied 11 km apart in the mid-Waimakariri basin. Soils at Puffers Stream, the main study site, ranged within 400m from a Recent soil on the youngest surface (T1) to a mature high-country Yellow-Brown Earth (HC YBE) soil on the oldest surface (T5). These soils, developed under 900 mm mean annual rainfall, were less leached and weathered than corresponding soils in the otherwise similar Craigieburn terrace sequence at Cave Stream (soils CB1-CB4; annual rainfall 1470 mm).

Soil chemical parameters were correlated with tussock and legume growth in field and glasshouse experiments to identify potential causal relationships. Natural and transplanted fescue tussock foliar yields were measured on the Puffers Stream soils and the effects of phosphorus (P), nitrogen (N), sulphur (S) and base cations (K, Mg, Ca) on tussock growth were assessed in the glasshouse. With the legumes, P amendment at rates between 0 - 400 kg P ha^{-1} was investigated at Puffers Stream and in the glasshouse. The effects of S, K, Mg, Ca addition and soil preparation for pot experiments were also examined.

Mature soils at Puffers Stream and Craigieburn are currently both mapped as Craigieburn HC YBE's, though physical and chemical differences are sufficient to warrant differentiation.

Fescue populations at Puffers Stream on T1-T5 ranged from 2.3 to 11.2 tussocks m^{-2}. Mean basal area ranged from 18 to 55 cm^2 and total tussock basal area from 163 to 246 cm^2 m^{-2}. Tussock basal area was closely related to shoot biomass (r = 0.949). Estimated tussock shoot biomass on T1-T5 ranged from 140 to 250 g m^{-2} and was greatest on soils with the highest P concentrations.

In 52 fescue tussocks from the main population on Puffers Stream T4, mean leaf length was 33.9 cm (range 23.6 - 48.3), mean flowering culm height 38.3 cm (range 23.0 - 66.0) and mean basal area 14.7 cm^2 (range 6.3 - 26.4). Tussock above ground biomass averaged 30.7 g DM (range 3.2 - 98.2) with an average composition of 23.5% live, 0.8% live-flowering, 46.4% recently-dead and 29.3% old-dead shoot DM. Mean live shoot tissue concentrations were 1.18 mg N g^{-1} (range 0.93 - 1.49), 0.62 mg P g^{-1} (range 0.25 - 0.92) and 0.56 mg S g^{-1} (range 0.44 - 0.77). Frequency distributions of tussock size, in 400 tussocks sampled from the same population, fitted by either negative exponential or power curve equations depended on the class size chosen to group tussocks and therefore appear of little biological value. Probably due to removal by grazing, the frequency of very small tussocks was less than expected in a naturally recruiting population.

Resident fescue tussock live blade N and P concentrations, monitored over two years on T1, T3 and T5, increased to a winter-spring maximum (1.77 mg N and 0.26 mg P g^{-1} DM) and decreased to a summer minimum (0.62 mg N and 0.09 mg P g^{-1} DM). Sulphur showed no consistent seasonal trend. Tussocks on the young recent soil, T1, had the highest shoot N concentration (mean 1.28 mg N g^{-1} DM) and on the oldest soil, T5, the lowest shoot P concentration (mean 0.12 mg P g^{-1} DM). Shoot sulphur concentrations were similar on all terraces.

Two years after transplanting cloned fescue tussock into T1-T5, tussock biomass was highest on T1 (0.86 g DM $tussock^{-1}$) and lowest on T5 (0.64 g DM). Transplanted tussock biomass and leaf length were closely related to those of natural tussocks on T1-T5 ($r = 0.832$ and $r = 0.899$). Consistent with the nutrient monitoring results, transplanted tussock biomass was greatest on soils with high N and P availability and lowest on soils with high exchangeable-aluminium levels.

In the glasshouse, P application with N caused the greatest increase in total fescue tussock biomass (5.8 g DM $tussock^{-1}$). Without phosphorus, K, Ca, Mg and S application as a basal fertiliser did not significantly increase growth above that in untreated soils (1.9 vs 1.8 g DM), nor did N application (1.9 g DM). Growth on unamended soils was greatest where soil P levels, principally organic P, were highest, but production was poorly related to transplanted tussock DM on the same soils in the field ($r = -0.260$).

Fescue tussock populations from Puffers Stream (T4) and Craigieburn (CB4) responded differently to edaphic factors suggesting ecotypic differentiation. Puffers Stream tussocks increased DM production 1.2 times with K, Mg, Ca and S basal fertiliser application and produced more DM on unamended soils with high P levels whereas Craigieburn tussocks did not respond to basal fertilisers and produced more DM on soils with high oxalate-extractable aluminium (Al_o). These differences between populations are consistent with specialisation for each soil leaching regime.

The N-fixing shrub Matagouri (*Discaria toumatou*), a co-dominant with fescue tussock at Puffers Stream, ranged from 0.8 to 1.6 plants m^{-2} on T1-T5 with a mean aerial volume varying from 0.04 to 1.6 m^3 m^{-2}. Matagouri volume was greatest on soils with high subsoil moisture availability and low levels of Al_o.

In a major legume field trial at Puffers Stream, transplanted lotus and clover seedlings on T1-T5 were monitored for four years. Lotus seedling mortalities were 13.0 % and clover 8.0 %. Seventy percent of all mortalities occurred on T1 and were attributed to low soil-water retention and resulting summer moisture deficit, principally in the first season during establishment.

Clover herbage yield the first season after establishment, averaged across all plots, was greater than lotus (176 vs 60 g m^{-2} DM). Herbage N and P concentrations were higher in clover (25.1 and 1.7 mg g^{-1} DM) than lotus (23.3 and 1.4 mg g^{-1} DM). Lotus yields exceeded clover yield in the two subsequent seasons, though yields progressively decreased (111 vs 56 and 84 vs 12 g m^{-2} DM).

All soils were P deficient and both legumes strongly responded to applied P, clover yield increasing 25.3 times and lotus 14.1 times from 0 to 400 kg applied P ha^{-1}. Lotus DM production per unit P applied, averaged over three seasons, was 1.5 - 1.6 times greater than for clover at rates of applied P between 0 - 50 kg P ha^{-1} whereas yield was similar to clover at 100 and 400 kg P ha^{-1}. Without applied P, clover yield was greatest on soils with higher P concentrations. Lotus yields were less strongly related to P availability.

In the glasshouse, lotus herbage yield, averaged across all treatments, was greater than for clover (15.6 vs 13.7 g DM pot^{-1}), though self-shading may have limited clover yield. Both legumes responded strongly to P, clover yield increasing 20.5 times and lotus 13.7 times between 0 and 400 kg applied P ha^{-1}. Lotus DM was markedly greater at low P rates than clover. Clover root: shoot production was 3.7 times greater than lotus without applied P but similar at 400 kg P ha^{-1}. The lower yield of both legumes on unamended Craigieburn soil (CB4), compared with the corresponding Puffers Stream soil (T4), was ascribed to higher soil P-adsorbtion reducing P availability and also to possible alumimium toxicity.

Lotus out-yielded clover with or without Ca, K, Mg and S basal fertiliser (21.5 vs 19.7 and 9.8 vs 7.7 g total DM pot^{-1}). Basal fertiliser increased lotus DM 2.2 times and clover DM 2.6 times, most probably by ameliorating sulphur deficiency. On unamended soils, yields of both legumes increased as soil exchangeable aluminium levels decreased.

As in the field trial, clover root and shoot N and P concentrations were higher than for lotus, with the greatest difference between the legumes occurring at low-P rates. P uptake in both legumes increased as soil P-retention decreased.

When lotus was grown in air-dried, sieved and potted T4 and CB4 soils and intact soil cores in a glasshouse trial, establishment was 1.3 times and herbage yield 1.7 times greater in sieved soils. Sieving lowered soil bulk density and increased the proportion of roots penetrating deeper in the soil. As N application removed differences in herbage production between sieved and intact soils, increased N mineralisation following air-drying and sieving was probably partly responsible for the increased growth on sieved soils. The difference in growth between sieved and intact Craigieburn soil was 2.6 times greater than between sieved and intact Puffers Stream soil. Pot trials results with these and similar soils cannot therefore be directly extrapolated to the field.

From these experiments it can be concluded that fescue tussock is a low-fertility tolerant plant with wide edaphic plasticity. The edaphic ecology of fescue tussock therefore appears that of a 'stress-tolerant competitor'. The edaphic ecology of 'Huia' white clover is typical of a ruderal-competitive plant suited to high fertility soils while 'Maku' lotus appears intermediate between a 'ruderal-competitive' plant which is tolerant of low fertility, acidic soils and a 'stress-tolerant ruderal'. Lotus is thus better suited than white clover for low-P situations in moderately acidic HC YBE soils.

Phosphorus, nitrogen and exchangeable aluminium appear the principal mineral elements determining both fescue tussock and legume growth. In addition sulphur is important for legumes.

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INTRODUCTION

INTRODUCTION

Short tussock grassland is the most extensive indigenous grassland association in New Zealand (Hunter & Blaschke 1986). Fescue tussock (*Festuca novae-zelandiae*) dominates the physigonomy of the montane short tussock grasslands through both islands. In a submission to the Tussock Grassland Research Committee, concerning research in the fescue tussock grasslands, Holloway (1954) wrote :

> *'... There appears to me to be one approach that has been neglected almost entirely; and to my way of thinking this approach is essential to any considerable advance in our understanding. There seems to me to have been no attempt made to conduct any thorough primary survey of the grasslands.'*

Thirty three years later, considerable advances have been made through such primary survey regarding the distribution and floristic composition of the fescue tussock grasslands and also in understanding fescue tussock's taxonomy, its breeding system, seedling establishment, seasonal growth pattern, and grazing and nutrient responses. Most studies, however, have been essentially descriptive and therefore the advance in understanding the auto-ecology of the tussock itself has been small.

To achieve any thorough ecological understanding of the fescue tussock grasslands, and the ecology of fescue tussock, is is necessary to go beyond description and establish the causal relationships and factors responsible for the behaviour of fescue tussock. However the search for correlation and causation raises what Harper (1982) terms the ecologist's trilemma of precision, realism and generality:

> *'The search for precision may lead him to work with unique genotypes in controlled environments designed to minimize the background of environmental noise. The risks are then that his experimental results have no realism because natural populations are usually genotypically polymorphic and environments are normally noisy. He may emphasize realism by studying the behaviour of individual plants in the field; then only very large and extended studies may allow significant effects to be detected.... The search for generality may sacrifice both realism and precision and lead the ecologist to large scale survey which runs the risk of yielding results which are only trite and superficial'.*

The aim of this thesis, nevertheless, is to investigate the edaphic ecology of fescue tussock on a representative range of high country and related yellow-brown earth soils. Two legumes, Lotus (*Lotus pedunculatus* cv. 'Grasslands Maku') and white clover (*Trifolium repens cv.* 'Grasslands Huia'), were also evaluated for their potential agronomic role in fescue tussock grasslands. To resolve Harper's trilemma, three complementary approaches were used :

Realism was sought by field study of the distribution and stature of the physiognomic dominants in fescue tussock grassland, fescue tussock and matagouri (*Discaria toumatou*), on a development sequence of different soils (Chapter 2) and by monitoring seasonal nutrient fluxes in resident tussocks (Chapter 3). Realism, with higher precision, was sought by field transplants of cloned tussocks (Chapter 4) and pre-grown lotus and clover (Chapter 6).

Precision was sought by experimental design with high replication and by repeating both field transplant experiments under controlled glasshouse conditions and experimental manipulation of mineral nutrition (Chapters 5 and 8).

To assess the departure from realism, large intact soil cores were compared in the glasshouse with identical, though disrupted, soils as prepared for use in standard pot experiments (Chapter 7).

Finally generality was sought by careful selection of contrasting soil development sequences spanning much of the pedological and climatic range found in the montane eastern South Island fescue tussock grasslands (Chapter 1). Generality was also sought by using widely used, standard legume varieties and comparing the edaphic responses of fescue tussock populations across one of the most important ecological gradients in the fescue tussock grasslands, precipitation.

Correlation with edaphic factors could be established from these studies, allowing generation of further hypotheses, requiring more precise testing, regarding the edaphic ecology of these species (Chapter 9).

SECTION 1 : THE STUDY AREA

CHAPTER 1 LEGUME PHOSPHATE RESPONSE ON A SEQUENCE OF HIGH-COUNTRY YELLOW-BROWN EARTH SOILS

1.1 LOCATION

The broad Study Area comprises the southern half of the mid Waimakariri Catchment between the Craigieburn, Torlesse and Puketeraki Ranges (Fig. 1.1). Specific comparison within the Study Area is made between two terrace sequences 11 km apart at Cave Stream (Craigieburn Site) and Puffers Stream, the main study site (43° 09'S 117° 43'E and 43° 09'S 171° 53'E : Grid references NZMS 1, S66:205 027 and :342 024; Plate 1).

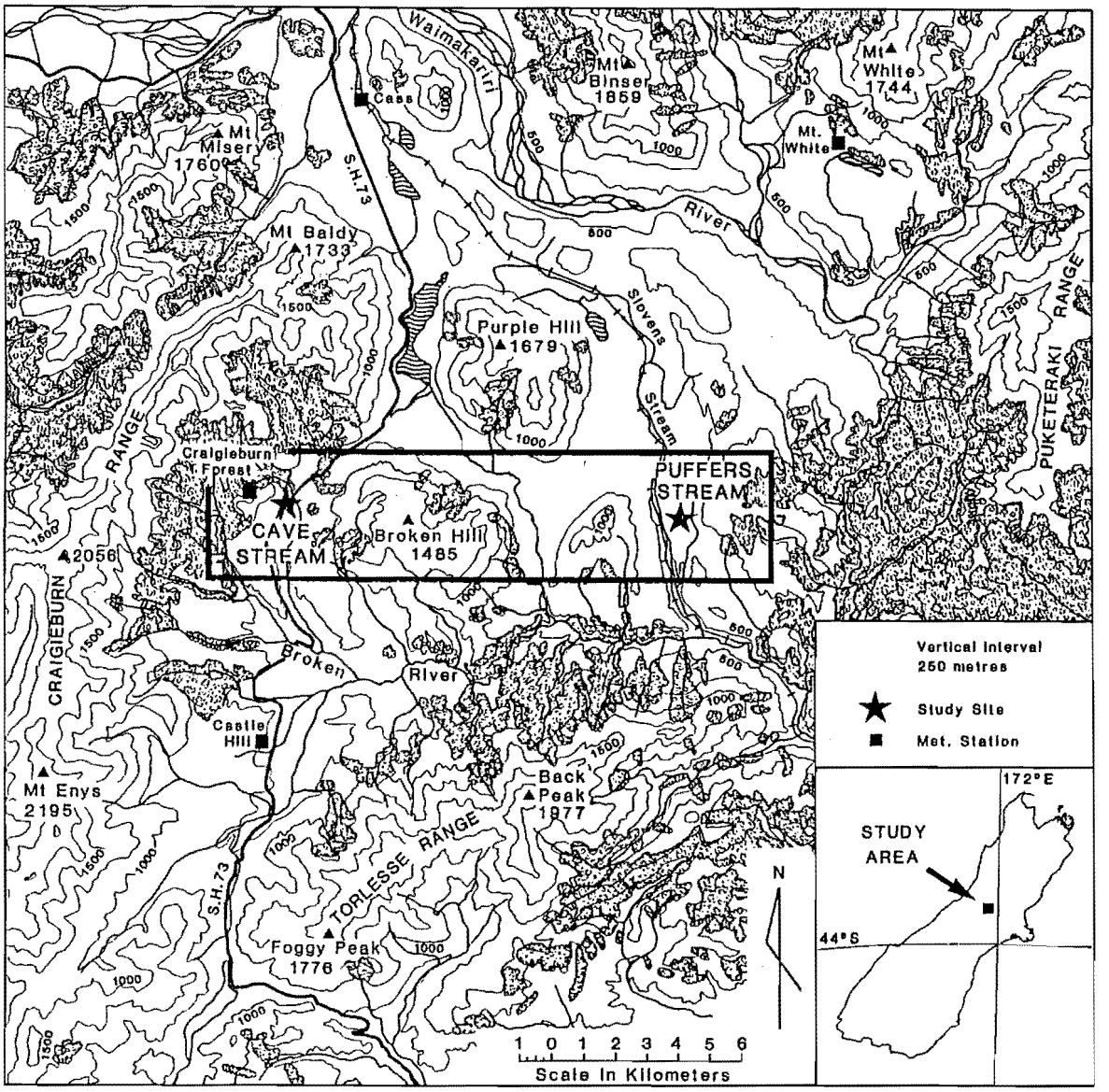


Figure 1.1 : The Study Area and Study Sites

The main divide of the Southern Alps lies approximately 35 km to the north west of the study sites with subsidiary ranges forming their immediate boundaries. The western boundary, the Craigieburn Range, rising to 2,200m, is 5 km to the west of the Craigieburn site and 17 km west of Puffers Stream. The Southern boundary, the 2000m high Torlesse Range is 10 km to the Southwest of Craigieburn and 6 km due south from Puffers Stream. The Puketeraki Range (1600 - 1800 m) lying 20 km east of Craigieburn and 10 km east of Puffers Stream, forms the basin's eastern boundary. The Mt White (1745m) and Savannah Ranges (1859m) form the immediate northern boundary before merging into the main divide. In addition, within the boundary ranges, block faulted massifs, Purple Hill (1680m), Broken Hill (1485m) and Nomans Land (1116m) are 5-8 km east/west of the respective study sites.

1.2 GEOLOGY AND GEOMORPHOLOGY

The Study Area lies within a complex tectonic depression bounded by major faults. Triassic sandstones are overlain unconformably by Cretaceous and Tertiary formations and late Pleistocene glacial deposits (Gage 1970; Fig. 1.2). Eighty percent of the catchment is mapped as Torlesse greywacke and associated sandstones, five percent as Tertiary sediments with volcanic intrusives and the remainder Pleistocene glacial and glacio-fluvial deposits derived from greywacke (Gregg 1964). The major formations occurring in the general Study Area are summarised in Table 1.1 and occurrence near Puffers Stream mapped in Figs. 1.3 and 1.4.

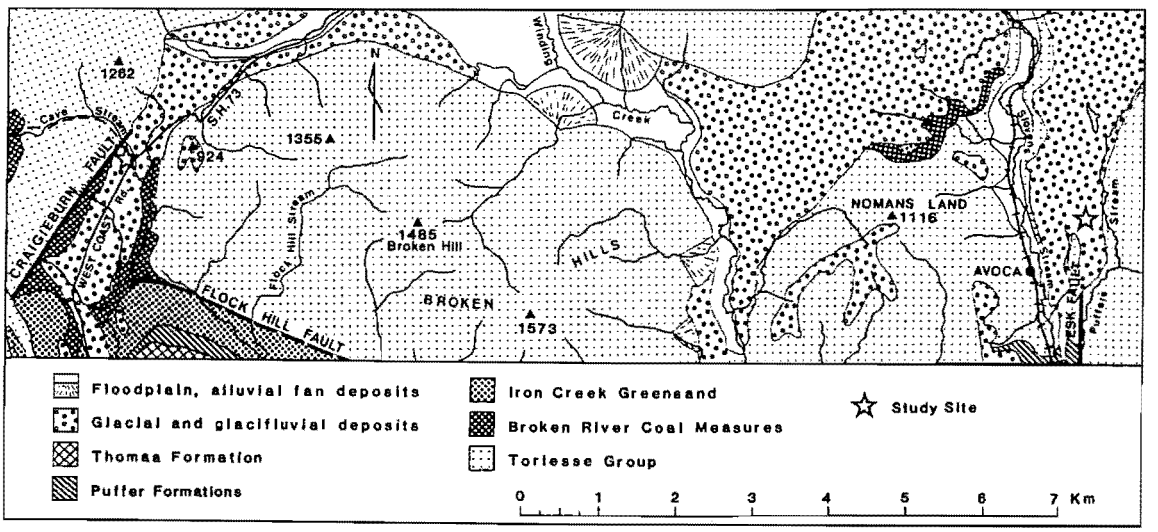


Figure 1.2 : Geology of the Study Area (Gage 1970)

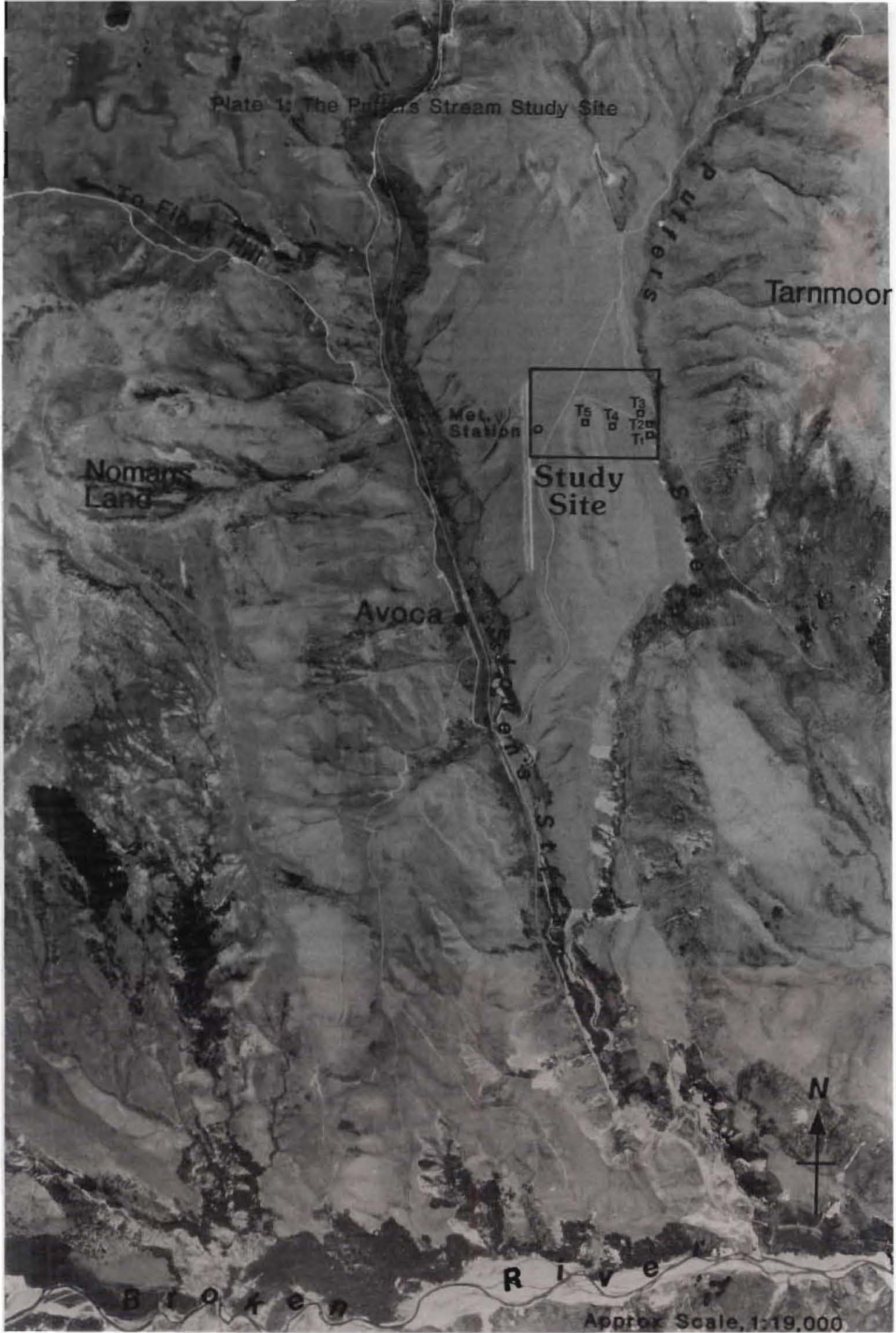


Plate 1: The Pr[illegible]s Stream Study Site
To Flo[illegible]
Tarnmoor
Met. Station
T5
T4
T3
T2
T1
Study Site
Nomans Land
Avoca
N
Approx Scale, 1:19,000

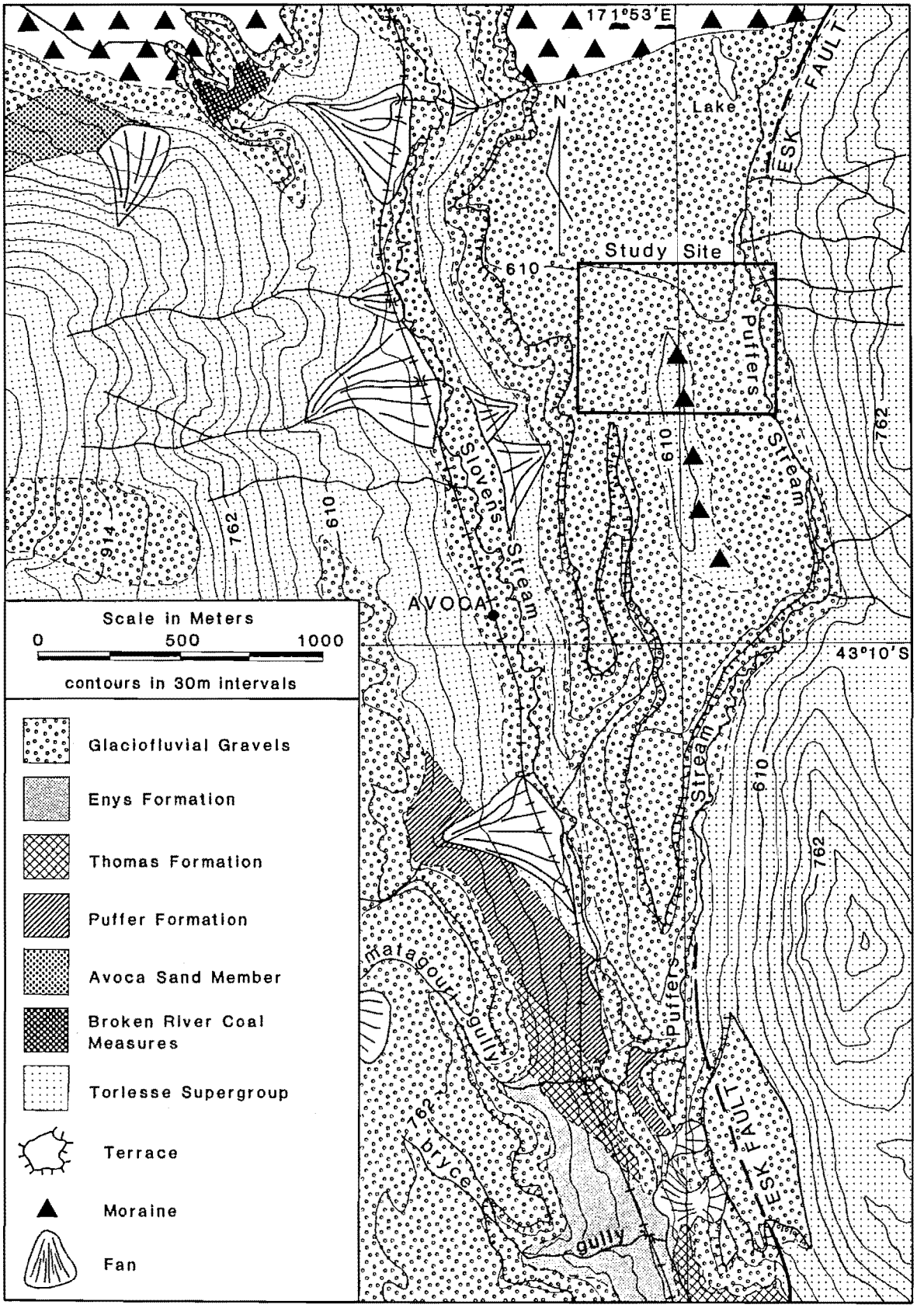


Figure 1.3 : The Geology of the Puffers Stream Site (McLennan 1981)

Table 1.1 Geological Formations in the Mid Waimakariri Basin.

Formation	Description	Age
Flood plain, alluvial fan deposits	Reworked Torlesse sediments.	Holocene
Glacial and fluvioglacial deposits	Reworked Torlesse sediments	Late Pleistocene
Enys Formation	Mixed marine/non marine siltstone /fine sandstone /cobble conglomerate	Miocene - ? Early Pliocene
Thomas Formation	Marine basaltic tuffs and limestone	Early ? - Late Oligocene
Coleridge/Puffer Formation	Marine Calcareous mudstone - glauconitic sand	Early Oligocene
Iron Creek Formation	Marine glauconitic - quartz sandstone	Late Cretaceous - Eocene
Broken River Coal Measures	Non-marine, quartzose sands, carbonaceous silts and coal	Late Cretaceous
Torlesse Suite	Marine, well indurated sand, silt and mudstone	Triassic

(after Gage 1970, Bradshaw 1975 and McLennan 1981)

The basement rock of the Study Area, the Torlesse Supergroup ('Canterbury Suite' Andrews *et al.* 1976) comprises the largest unit of sedimentary rock in New Zealand. It has been intensively studied, particularly in the South Island (Andrews *et al.* 1976, Gage 1980).

Torlesse rocks are predominantly medium to fine grained quartzose-feldspathic sandstones (greywacke) varying to bedded silt and mudstones (Bradshaw 1977, Andrews *et al.* 1976, MacKinnon 1980). Detailed examination of Torlesse rocks at Broken River, 5 km from the western margin of the Study Area, demonstrated three sedimentary facies of thick bedded sandstone, thin bedded siltstone and black mudstone with one putative volcanogenic facies of interstratified chert and shale (Andrews 1974).

Petrological analysis shows the mineral assemblage of Torlesse rocks at Broken River to be very similar to Torlesse rocks at Camp Stream, 2.5 km northwest of Cave Stream (Furkert *et al.* 1975) and Arthur's Pass, 30 km north of the Study Area (MacKinnon 1980). Torlesse petrology is reasonably similar elsewhere throughout New Zealand (Reed 1957, McGregor 1963, Dickinson 1971, Bradshaw 1972).

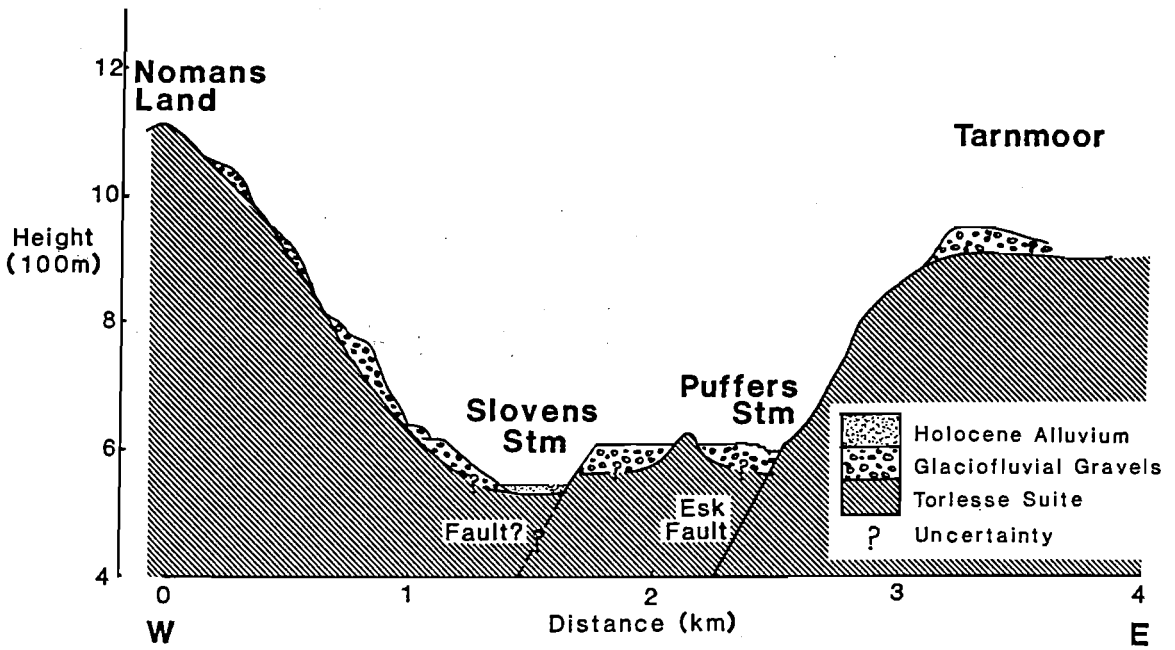


Figure 1.4 Geological Stratigraphy of the Puffers Stream Site

Torlesse rock fabric at Broken River consisted of clastic grains, sand sized or less. Mono- and polycrystalline quartz comprised 40-50%, plagioclase feldspar 12-14%, penecontemporaneous sedimentary fragments of intra-basinal mudstone 6-8%, plutonic fragments 4%, foliated metamorphic and volcanic rock fragments 0-3%, Chlorite 3%, biotite 3% and hornblende, epidote, zoisite, ilmenite, and garnet totalling between 2-6% . The sediments appeared to have been derived largely from grandiorite during the late Paleozoic and Mesozoic (Andrews 1974).

Torlesse composition at Camp Stream was reasonably similar (Furkert *et al.* 1975). Composite samples from fresh scree detrius comprised 31% quartz, 42% feldspar, 6.6% chlorite, 7.0% illite, 5.0% amorphous minerals, 2.5% vermiculite and 2.0% inter-layered hydrous mica and montmorillonite.

Broken River intrusive volcanic dykes occur sparsely 5 km south of the Avoca site (McLennan 1981). Gage (1970) gives their following average composition :

phenocrysts	pyroxene	9.6%
	olivine	4.8%
groundmass	plagioclase	41.1%
	pyroxene	28.4%
	ore	8.3 %
	glass	7.8%

Analyses were very similar to other basaltic flows and dykes in Canterbury (Gage 1970).

The late Cretaceous and Tertiary rocks have been intensively investigated (Gage 1970, Bradshaw 1975, McConchie and Lewis 1978, McLennan 1981, McLennan and Bradshaw 1984), but are absent or overlain at the primary study sites.

Quaternary glacial events in Canterbury are summarised in Table 1.2 with limits of the late Pleistocene advances in the Waimakariri shown in Fig. 1.5. The earliest glaciations were the most extensive. Avoca ice extended as far as Racecourse Hill near Sheffield, leaving within the basin high outwash near Avoca, now deeply eroded (Gage 1958). Woodstock and Otarama advances reached as far as the lower Waimakariri gorge but did not extend far into the Castle Hill basin (Gage 1977) Little evidence of either remains. Wood fragments in silts between Otarama and Woodstock Outwash at Joyces Creek are aged as > 45,000 yrs B.P., (Moar and Gage 1973) and date the Woodstock/Otarama interglacial.

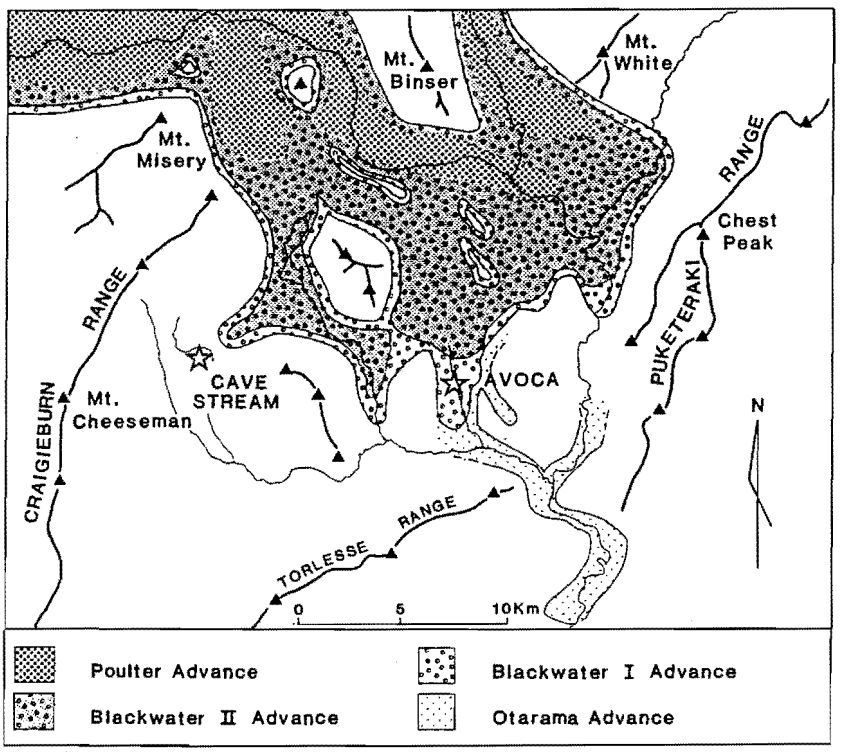


Figure 1.5 Extent of Pleistocene Glaciations in the Waimakariri (after Gage 1977)

Table 1.2 Correlation of Glacial Chronologies in Canterbury.

GLACIATION	Age (yr)	Mackenzie Basin	Rangitata Valley	Rakaia Valley	Waimakariri Valley
	< 11,950		*INTERGLACIAL*		
OTIRAN		Tekapo Advances	Spider Lakes-Lake Heron	Acheron Advances	Poulter Advances
	< 19,750		*MINOR INTERSTADIAL*		
		Mt John Advances	Hakatere-Emily	Bayfield Advances	Blackwater Advances
	> 45,000		*MAJOR INTERSTADIAL*		
WAIMEAN	130,000 ?	Balmoral Advances	Trinity Advances	Tui Creek Advances	Ōtarama Advances
			INTERGLACIAL		
WAIMAUNGAN	250,000 ?	Wolds Advances	Dogs Hill Advances	Woodlands Advances	Woodstock Advances
			INTERGLACIAL		
PORIKAN	500,000 ?	pre-'BOG' ?	Pyramid Advances	?	Avoca Advances

(after Mabin 1980, Gage 1980)

Precisely when the Blackwater advances began is unknown. There were two major advances, separated by a minor recession, with probably a third minor advance (Gage 1958 1977). Gage postulates that the first advance began about 26,000 yrs. B.P. (Gage 1980). Lake deposits found in the Lyndon-Acheron valley 15 km southwest of the Cave Stream site, allow dating of the Blackwater III / II interstadial (Soons and Burrows 1978, Table 1.3).

Table 1.3 Correlation of Glacial advances in the Waimakariri and Rakaia Catchments

Year BP	RAKAIA	WAIMAKARIRI
< 19,750	Bayfield III	Blackwater III
19,750 - 22,800	*RECESSION*	
> 22,800	Bayfield II	Blackwater II
? 26,000	Bayfield I	Blackwater I

(after Soons and Burrows 1978)

The last Blackwater pulse ended about 18,000 years ago with the smaller Poulter advances beginning about 16,000 yrs. B.P. and ending about 13,500 yrs. B.P.(Gage 1977, Burrows 1983). Minor advances since the Poulter recession occurred in the Alpine zone between 11,000 - 8,300 yrs. B.P.(McGrath), 5,600 - 4,000 (Arthurs Pass), 3,000 - 800 (O'Malley) and within 550 yrs. (Barker) (Chinn 1976).

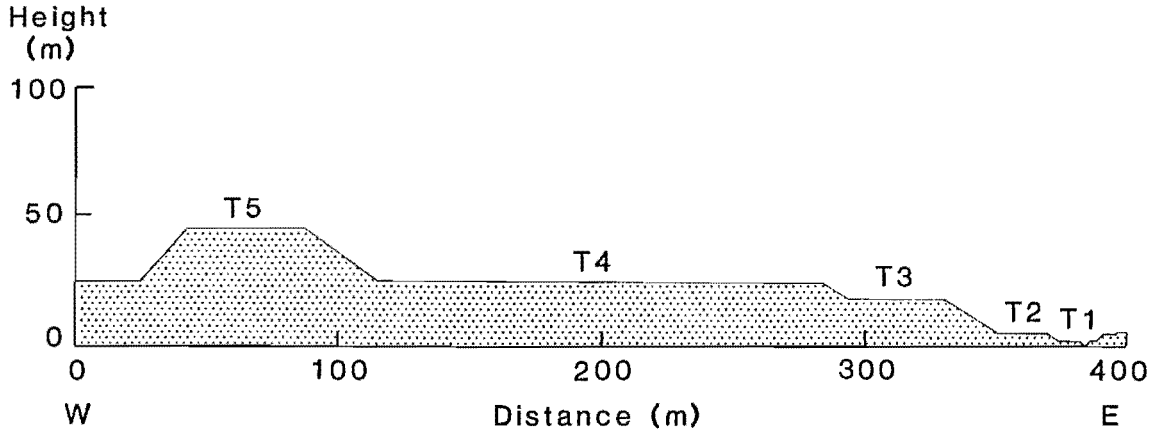
The Cave Stream site was not glaciated during the Blackwater advances (Gage 1977, G. Howard, pers. com. 1986) though ice advanced to within 1 km (Fig. 1.5). The main surface at Cave Stream, CB4, was formed as quartzose-feldspathic fluvioglacial gravels, derived from Torlesse sandstone and siltstone (Furkert *et al.* 1975), were deposited in a large proglacial meltwater stream draining through the Craigieburn saddle to Broken River. Following glacial recession, Cave Stream subsequently incised four terraces, CB1 to CB4 (Frontispiece). The uppermost terraces, CB3 and CB4, were mantled with 40 - 60 cm of loess, derived either locally or from the Waimakariri 10 - 15 km to the north. The maximum rate of loess accumulation probably occurred after ca 7,000 yrs. B.P. (Tonkin 1981).

The Puffers Stream site is a similar but more complex sequence of surfaces (Fig. 1.6). The main surface at Puffers Stream, T4, is very similar to CB4 at Cave Stream, being formed by fluvioglacial outwash from the terminus of the Slovens Stream lobe of the Waimakariri glacier 1 km due North (Fig. 1.3). Puffers Stream subsequently incised a small flight of four terraces (Plates 3 and 4).

However, there are differences in geomorphology between the two sites. The oldest surface at Puffers Stream, T5, is a greywacke ridge rising 10 - 30 m above the main surface (Fig. 1.6). A volcanogenic facies of interstratified chert and shale, similar to outcrops elsewhere in Broken River (Andrews 1974), surfaces at the eastern margin of the ridge. Morainic boulders and fluvioglacial gravels cap the ridge to the west and are probably best assigned as late Blackwater I deposits.

The second (T2) and third (T3) terraces are incised in well sorted fine to medium angular greywacke fragments deposited by a small debris flow from a gully 50 - 100 m to the west over the fluvioglacial gravels re-exposed in T1. Brundall (1966) and Pierson (1980, 1981) describe the deposition, stratigraphy and characteristics of such flow deposits in Cass and similar Canterbury sites. Varying thicknesses of loess (20-60cm) cover the three upper surfaces.

Plate 2 Puffers Stream : the main fluvioglacial outwash surface (T4).



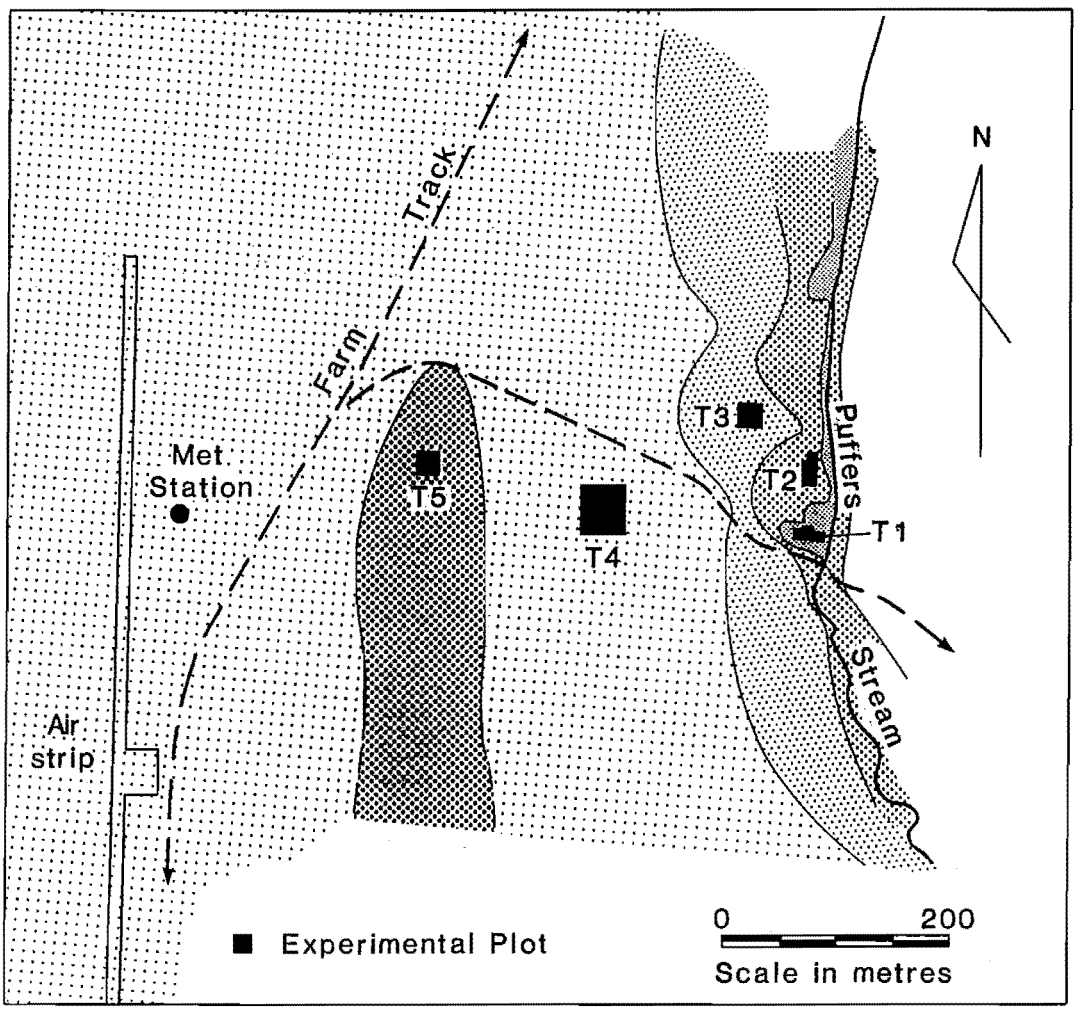


Figure 1.6 : The Puffers Stream Study Site
(a) Site map
(b) Site cross section

Plate 3 : The Puffers Stream Terraces T5-T4

Plate 4 : The Puffers Stream Terraces T1-T4

1.3 CLIMATE

1.3.1 General

The climate of the upper Waimakariri basin is predominantly influenced by the location of the surrounding mountain ranges and the regular eastward movement of successive anticyclones and low pressure troughs across the Tasman Sea (de Lisle 1966 1969, Coulter 1967).

Anticyclonic weather is usually fine with light winds. As a subsequent trough approaches, cloud cover and westerly winds increase in the Southern Alps. When the trough rises over the Alps, it cools, with precipitation peaking in the western ranges and decreasing to the east (McSaveney 1978, Griffiths and McSaveney 1983). The dry airflows descending the lee slope of the Alps are warmed by pressure change and are comparable to Chinook or Fohn winds. After the cold front in the trough has passed, winds normally turn to the south, temperatures drop, and further precipitation may occur. The trough is usually replaced by another anticyclone bringing settled weather. De Lisle (1969) estimates the average time between high pressure systems at about a week.

The climate of the upper Waimakariri is one of the most intensively studied upland climates in New Zealand. Precipitation records from 1918 are available from the University of Canterbury field station at Cass (Greenland 1977). Daily precipitation has been recorded since 1964 at the Chilton Valley 1.5 km from the Field station. In 1954 the New Zealand Forest Service established two meteorological stations at 914m and 1550m in the Craigieburn Range 12.5 km and 14 km due east of Puffers Stream. Daily climatic data have been collected since 1964 at 914m and 1966 at 1550m (Morris 1965, Morris and O'Loughlin 1965 and McCracken 1980). Additional information is available from many short term studies, eg. Greenland and Owens 1967, Greenland 1973a,b, Benecke *et al.* 1976, 1981, Stevenson 1981, Turton 1982, Sturman 1983, McGregor 1984. Climatic information for the basin has been summarised by Hayward (1967), Greenland (1977) and the North Canterbury Catchment Board (1986).

1.3.2 Climate at the Study Sites

The macroclimate at the Cave Stream site (793m) is very similar to that recorded at the N.Z. Forest Service Craigieburn Forest Meteorological Station (914m) only 1 km due east. Cold air drainage, similar to that observed at Cass (Greenland 1977), would result in lower temperatures at the site and the topography suggests it would be exposed to a greater frequency and intensity of northerly winds. Other differences are likely to be small.

Plate 5 Meteorological Station: location on T4 from T5

Plate 6 The Meteorological Site in winter (photo: R. Harrison)

No detailed climatic data were available for Puffers Stream. Lying in the rain shadow of Mt. St. Bernard to the immediate northwest, and the Torlesse and Puketeraki Ranges to the south and east, it is probably one of the driest parts of the upper catchment. A short term meteorological station was established in 1981 to extend information on climatic gradients in the basin. The station was registered with the New Zealand Meteorological Service as 'Avoca' (reference N.Z.Meteorological Service, Christchuch, File 20/10/1) and officially inspected on 30 March 1983.

1.3.2.1 Methods

(a) Site

The meteorological station was located in a 9m x 9m fenced enclosure on the main terrace in the centre of the Slovens Stream valley. (Latitude : 43 09. 5'S, Longitude : 171 52.7'E, Grid Reference : NZMS1 S66 338 022, height above M.S.L. 594m, Plates 5 and 6). The site is flat fescue tussock grassland. To the west, 200m away, the terrace drops steeply 100m to Slovens Stream (Plate 2; Fig. 1.4). Six hundred metres to the west the valley rises sharply towards Nomans Land (1116m). To the east 150m away, is a small ridge rising 20-30m above the station. Beyond this, 700m east of the station, the valley rises steeply to Tarnmoor (945m). The terrace continues unobstructed to the north and south.

A standard white louvered Stevenson's Screen 1.2m above ground level was securely positioned in the centre of the exclosure. A small 1.5m x 1.5m x 2m aluminium chart shed was located on the western edge of the enclosure 1.5m from the screen. A 10.2m telegraph pole was installed 3m due west of the exclosure.

(b) Instrumentation

Instrumentation comprised :-

(1)	Screen Air Thermometers	(a)	Zeal Dry Bulb Sheathed Maximum and Minimum vertical mercury thermometer.
		(b)	Dry Bulb Sheathed horizontal mercury Maximum thermometer.
		(c)	Dry Bulb Sheathed horizontal alcohol Minimum thermometer.
		(d)	Dry Bulb Sheathed vertical mercury thermometer.
			Accuracy: All ± 0.1 ^{0}C
(2)	Earth Thermometers	(a)	2cm Right-angled Sheathed mercury thermometer.
		(b)	50cm Dry Bulb mercury thermometer,
		(c)	100cm lowered to depth in 2cm diameter PVC Tube.
			Accuracy: All ± 0.1 ^{0}C

		(d)	2cm 3 pen mercury in lead Lambrecht 10cm remote recording thermograph. 20cm 30 day drum chart. Probes positioned vertically in earth 2m North of screen.
			Accuracy: All ± 2%
(3)	Screen Thermohygrograph		Ota Keiki Seisakusho bimetallic thermograph and hygroscopic humidity sensor. 7 day clock. Positioned in screen.
			Accuracy : Relative humidity ± 5.0%; : Temperature ± 1.5%.
(4)	Direct Solar Radiation Recorder		Ota Keiki Seisakusho bimetallic Actinograph. 7 day clock. Positioned level on top of screen.
(5)	Anemometer		Lambrecht mechanical directional anemometer. 30 day clock. Mounted on 10.2m mast.
(6)	Precipitation	(a)	10.2cm diameter plastic Marquis manual raingauge, orifice level, 35cm above ground, 18m due North from exclosure.
		(b)	Ditto. Positioned 1.5m N.E. from screen inside exclosure.
		(c)	Ditto. Positioned 50cm due west of (b). This gauge maintained with 2cm kerosene.
		(d)	Grey board inserted flat at ground level for base measure of accumulated snow depth.

In addition, a Munro Cup counter anemometer was located on top of the small ridge to the east of the exclosure (Grid Ref S66: 340 022). The anemometer was mounted on a 2m steel mast, firmly guyed, at one corner of the experimental plot (T5). An identical anemometer was similarly located on the lowest terrace, T1 (Grid Ref: 343 022; Plate 4).

The Stevensons Screen was erected on 21 January 1981 and a Lambrecht thermograph installed. On 29 May 1981 an additional Otakeikei Thermohygrograph was installed. It was read until the 3 July 1983. A Zeal maximum and minimum thermometer was added on 7 May 1981 and read until 3 July 1983. Standard mercury maximum and alcohol minimum thermometer were installed on 20 July 1982. A 3 pen soil thermograph was installed on 10 March 1981 and read until 20 April 1984. Weekly temperature readings of 50cm and 100cm began on 26 July 1982 and ceased on 20 April

1984. The actinograph operated continuously from 24 November 1981 until 3 July 1983, except for a calibration check from 24-27 April 1982.

The first raingauge was installed on 1 January 1981, the second on 7 May 1981 and the third on 22 February 1983. Gauges were read until November 1983.

A 10m telegraph pole was erected on 20 February and the anemometer mounted on a 5cm diameter x 20cm base pipe. The anemometer was connected to a cassette recorder data logger, powered by 6 volt batteries and charged with a solar panel. Unfortunately, the data logger was unreliable, particularly at low temperatures, and only fragmentary data was recovered. The system was replaced with a Lambrecht chart recorder anemograph on 20 January 1982 and operated continuously (except from 11 February to 3 March and from 30 November to 7 December 1982) until removed on 1 December 1983. The 2m Munro Cup counter anemometers were installed on 9 June 1981 on Terrace 5, and on 2 July on Terrace 1.

Instruments were usually serviced every 6-8 days, from January, 1981 to July, 1983 and thereafter monthly to December, 1983.

Instruments were calibrated and checked as follows :

(a) Screen Air and Earth Thermometers. Checked against a standard thermometer at Lincoln College before use. All thermometers were rechecked in the field on 30 March, 1982 against a standard N.Z. Meteorological Service thermometer. All thermometers read within 0.1 ^{0}C of the standard thermometer.

(b) Three pen Earth Thermograph, Hygrothermograph. These were serviced and calibrated by the Ministry of Works and Development, N.Z. Hydrological Services Depot, Belfast, immediately prior to field use. The thermograph probes were extracted and positioned in parallel in a snow packed box on 19 July 1982. All three probes recorded -0.8 ^{0}C, compared with -0.6 ^{0}C from a standard thermometer. The probes were returned without change. The Hygrothermograph was checked periodically against instruments from Lincoln College and against maximum and minimum Dry Bulb thermometers.

(c) Solar Actinograph. This was calibrated against the Lincoln College Eppley standard pyranometer (Appendix 1.1).

(d) Anemometers. The Lambrecht totalising anemometer was serviced and calibrated by the Ministry of of Transport, N.Z. Meteorological Service, Wellington, immediately prior to field installation. The Munro Cup counter anemometers were calibrated using Lincoln College and D.S.I.R. Civil and Industrial Development Division wind tunnels. (Appendix 1.2).

(e) Manual Raingauges. Comparison of precipitation in gauges a,b and c assessed differences between gauge position and also evaporative loss.

(c) Analysis

Precipitation was recorded approximately weekly but analysed, as standard, for a period extending from 9 am on the previous day to 9 am on the day when the gauge was read. However, if the gauge was read later than 9 am, the half hourly records from Cass station were used to partition the precipitation to the correct period for each day. Similarly, the Cass data was used to partition monthly rainfall when the weekly readings spanned a change in month. These procedures were necessary to accurately compare data with that from other stations.

To establish precipitation patterns in the mid Waimakariri, daily precipitation records from 1981 - 1983, at Cass and Craigieburn Forest were totalled for the same periods as the Avoca. Unfortunately, the Craigieburn Forest gauge underestimated precipitation due to snow by as much as 80% (July 1983) and required correction using an adjacent Belfort weighing bucket raingauge. Records were amended whenever the Belfort exceeded the manual gauge by 6.0mm. Observer recording errors, some considerable, were corrected by the Belfort and Ministry of Works gauge at Camp Stream. Excepting such instances, there was excellent agreement between the two instruments ($r = 0.986$).

The Cass Lambrecht Recording Raingauge (Sturman and Soons 1984) was checked by comparing precipitation recorded on chart with the actual precipitation stored in a reservoir. Monthly differences ranged between - 12.1 to 11.8 mm in 1983 and - 5.2 to 14.0 mm in 1984. Overall, there was close agreement :-

1983	Chart	= - 4.745	+	1.075	Reservoir	($r = 0.991$)
1984	Chart	= 5.669	+	0.993	Reservoir	($r = 0.993$)

In addition, monthly data from Castle Hill and Mt White (N.Z. Meteorological Service, 1981, 1982, 1983) were used to establish correlation with precipitation elsewhere in the Basin.

Solar radiation charts were digitised by computer at the Forest Research Centre, Ilam. Areas were converted to incident solar radiation per day using the actinograph calibration equation (appendix 1.1) and time.

Twenty nine days were selected by random number and re-digitised to check digitising accuracy. Re-measurement differences were extremely small. The mean difference was 0.04 MJ/day with a maximum absolute difference of 1.6 MJ/day. The close fit of the regression line to the expected intercept of zero and regression coefficient of unity shows there was no bias in remeasuring either large (summer) or small (winter) areas :

Repeat = - 0.08 + 1.02 Original ($r = 0.995$)

To show month variation in precipitation intensity, wind direction and windspeed, data were fitted using spline smoothing by the statistics package SAS (SAS Institute 1986).

1.3.2.2 Results

(a) Precipitation

There was no significant difference in precipitation recorded inside or 18 m outside the meteorological exclosure on T4 (Avoca). For 100 paired readings, 1981 - 1983, mean precipitation recorded inside the exclosure was 17.4mm (0.2 Std. Error of Mean) compared with 17.2mm (0.2 SEM) outside. Evaporative loss in unprotected gauges was negligible. There was no significant difference between gauges with or without kerosene : mean 39.9mm (13.1 SEM) vs 38.7mm (12.4 SEM).

Precipitation at Avoca differed between years ($p < 0.05$). Mean annual precipitation was similar in 1981 and 1982 (799.0mm and 809.5mm) but wetter in 1983 (1105mm). Monthly precipitation also differed significantly ($p < 0.001$, Fig. 1.7).

Rainfall intensity was not measured at Avoca therefore unpublished Cass data were used, courtesy of Dr A.P. Sturman, University of Canterbury (Fig. 1.8). Precipitation intensities were normally very low with a rate of 3mm / half hour being rarely exceeded. Intensities at Avoca are likely to be very similar to those at Cass.

Snow was recorded only when visiting at the site; 6cm on the 26 July (Plate 6) and 1.5cm on the 23 October 1982. Short duration falls occurring between weekly servicing were not recorded, so snow precipitation was almost certainly greater than reported.

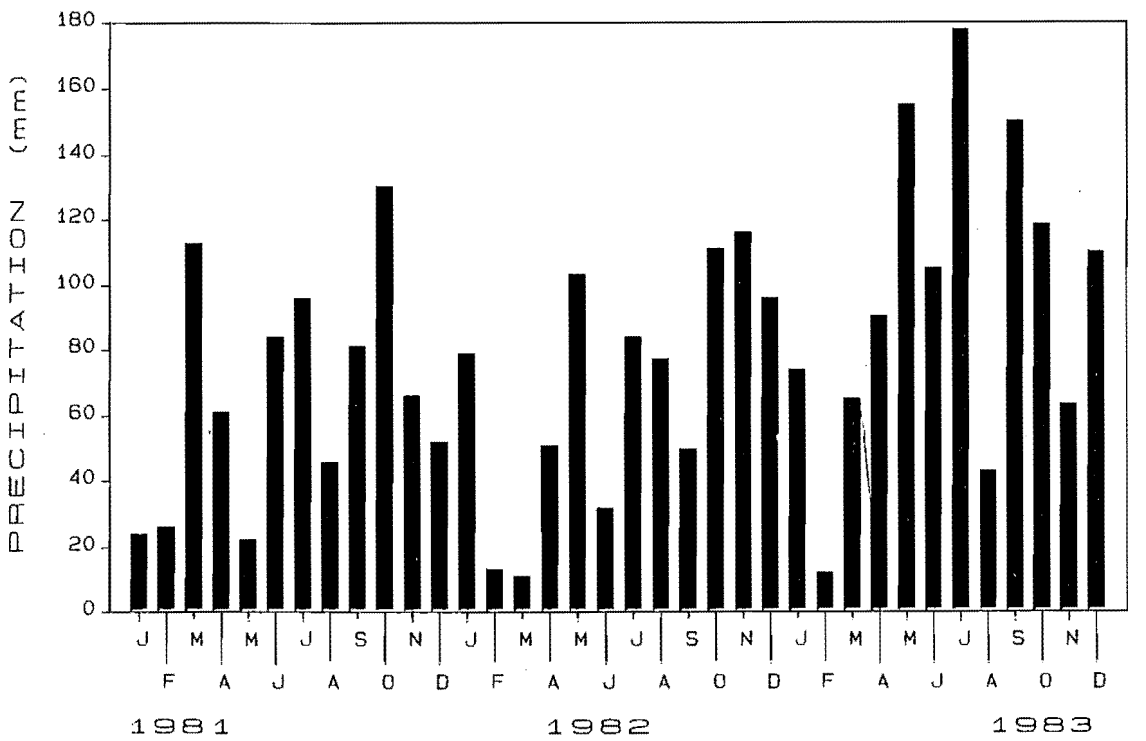


Figure 1.7 Precipitation at Puffers Stream 1981 - 1983.

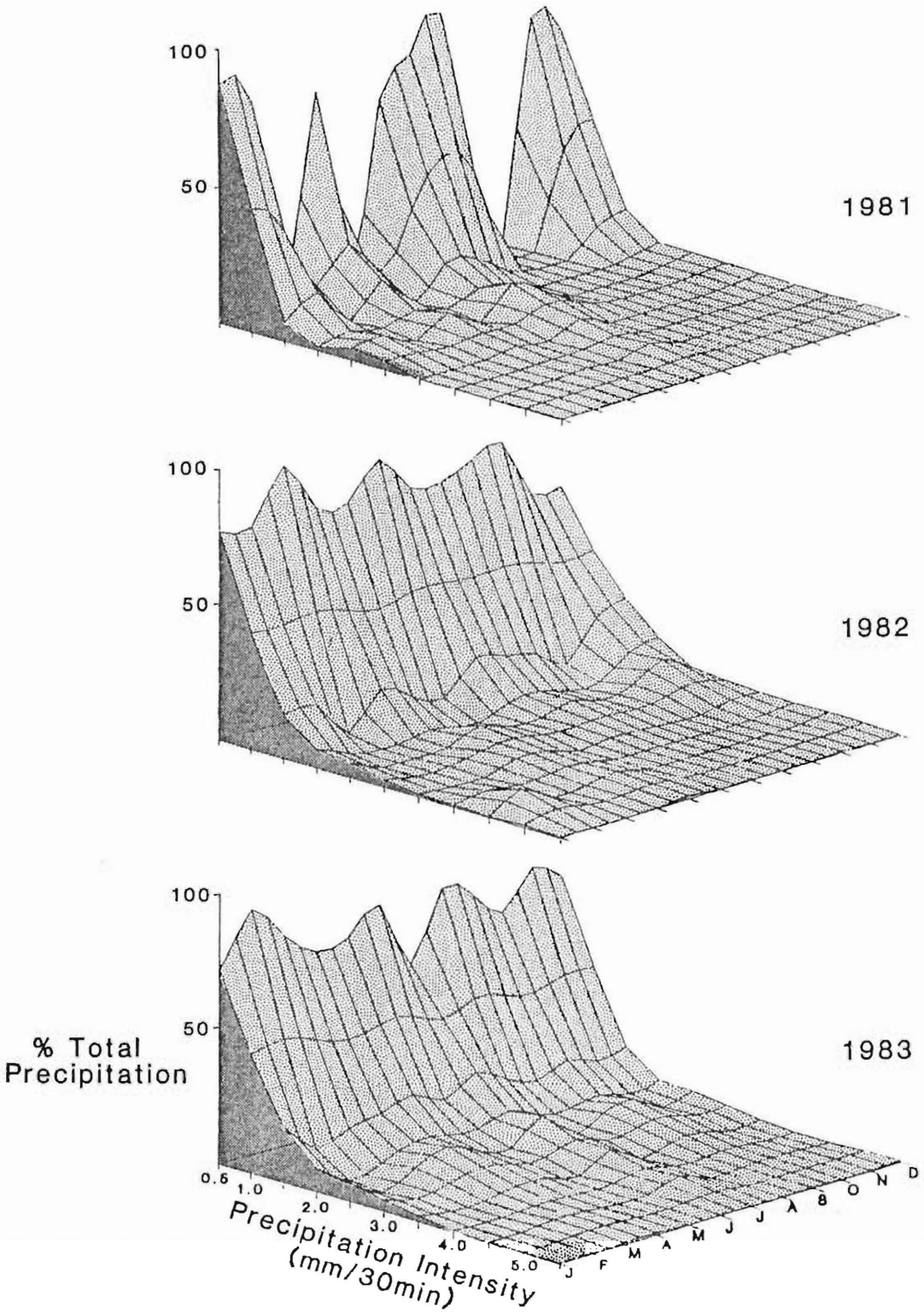


Figure 1.8 Precipitation intensity at Avoca 1981 - 1983.
(Missing data responsible for depressions in 1981)

(b) Wind

As expected, wind run at 2m on the two terraces was closely related. During 2 July 1981 to 25 May 1982 the relationship was:

T1 Wind Run (km) = 133 + 0.627 T5 Wind Run (r= 0.983)

Wind speed was significantly higher on Terrace 5 than on Terrace 1 ($p < 0.001$). The mean wind velocity on T5 was 4.70 m/s (0.23 SEM) and only 3.22 m/s (0.17 SEM) on T1 (Fig. 1.9) the difference being almost certainly directly due to topographic sheltering. Mean monthly wind velocity speeds ranged from 1.02 m/s to 6.34 m/s on T5, and 0.7 m/s to 4.35 m/s on T1 with a clear summer maximum and winter minimum (Fig. 1.10).

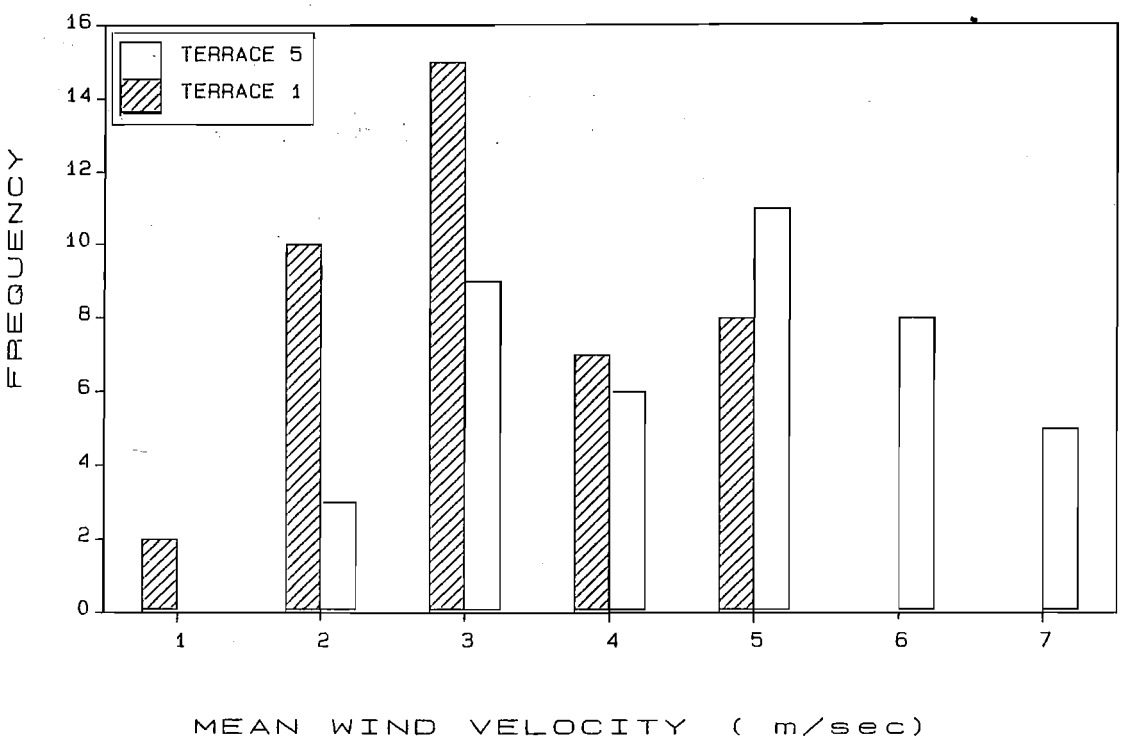


Figure 1.9 Windspeed frequency distribution on T1 and T5

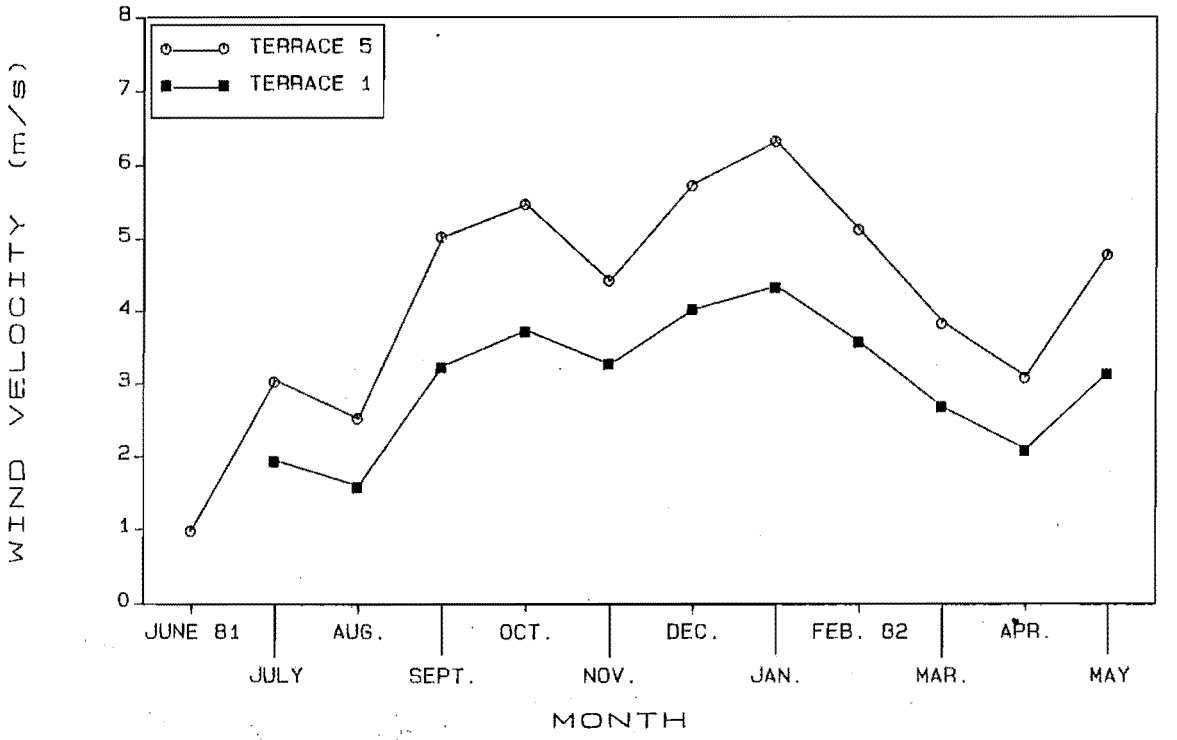


Figure 1.10 Mean monthly windspeed at 2m T1 and T5 June 1981 - May 1982.

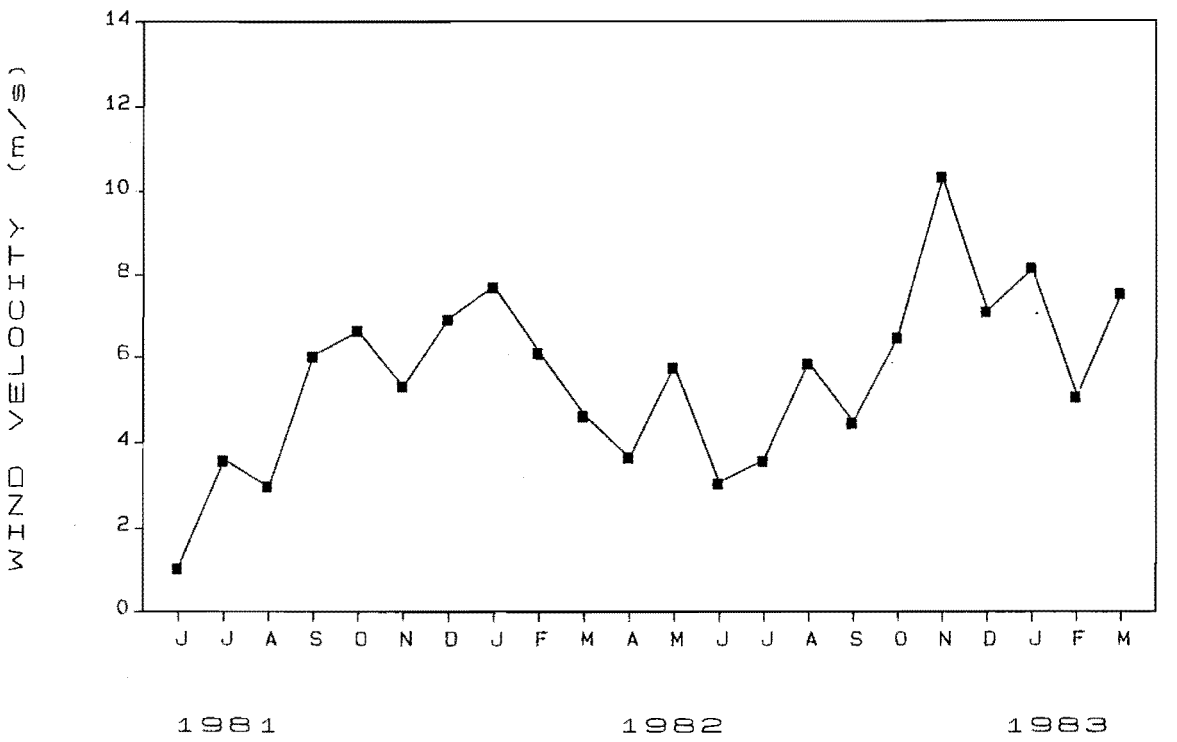


Figure 1.11 Mean monthly windspeed at 10m, Puffers Stream 1981 - 1983.

Wind velocity recorded at 10 m at the main meteorological station was higher, but very closely related to wind velocity at 2m on T5. A direct linear relationship between the two heights held between mid-summer through to mid-winter (26 January to 25 May 1982) :-

WR 2m (km/hr) = 127.4 + 0.811 WR 10m (r = 0.998).

This relationship was used to convert 2m data to extend the data available for plotting seasonal windspeeds.

At the main meteorological station mean monthly wind speed ranged from 1.08 m/s (July 1981), to 10.3 m/s (November 1982). The extreme minimum and maximum wind speeds were 0.0 m/s (March, August, September, December 1981) and 27.1 m/s (March 1982). There was a well defined winter minimum and spring - summer maximum (Fig. 1.11)

Analysis of the 1982 data, the only year with complete 10m data, showed striking diurnal variation in wind velocity (Fig. 1.12) and strong predominance of northerly airflows (Fig. 1.13). Airflows from the south and southeast were less frequent while airflow from the east and west rarely occurred. Seasonal variation in wind direction was marked (Fig. 1.14).

While the frequency of northwesterly winds is comparatively low, their intensity is easily appreciated by examining mean monthly wind speeds (Fig. 1.15). The mean velocity of northerlies and northwesterlies increases through spring to peak in early summer. In contrast, southerly or southeasterly winds are more consistent through the year but seldom exceed 20 km/hr. Wind velocities are at a minimum near mid Winter.

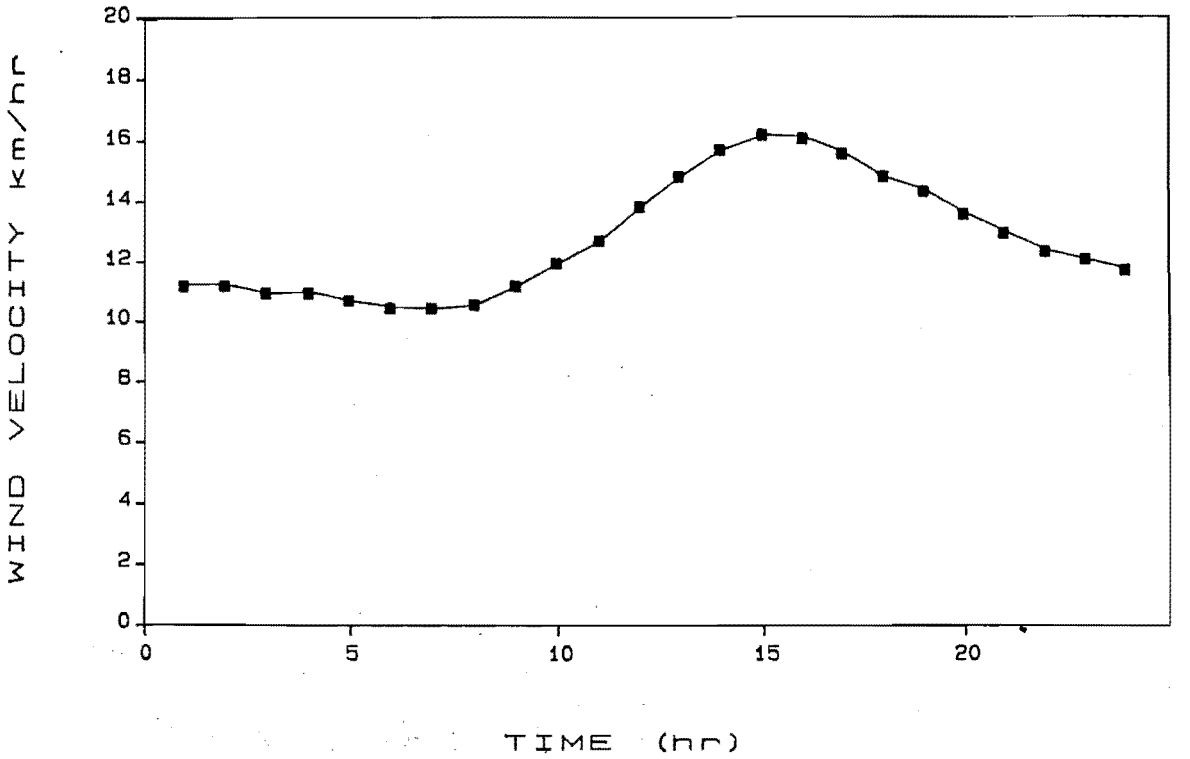


Figure 1.12 Diurnal variation in windspeed at 10m Puffers Stream 1982.

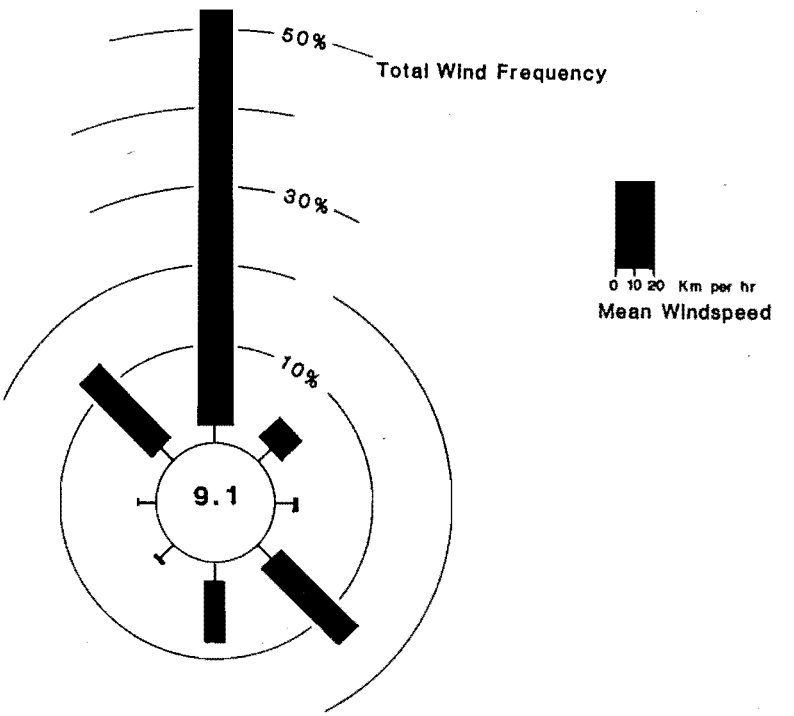


Figure 1.13 Mean monthly wind direction at 10m, Puffers Stream 1982.

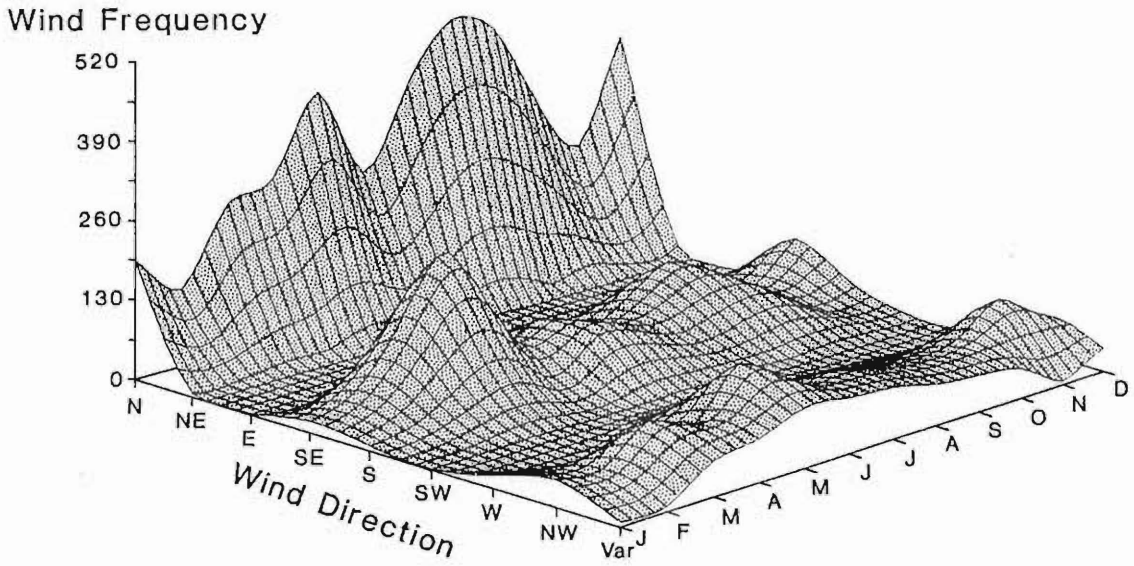


Figure 1.14 Seasonal variation in wind direction at 10m, Puffers Stream 1982. (Var. = Variable wind direction)

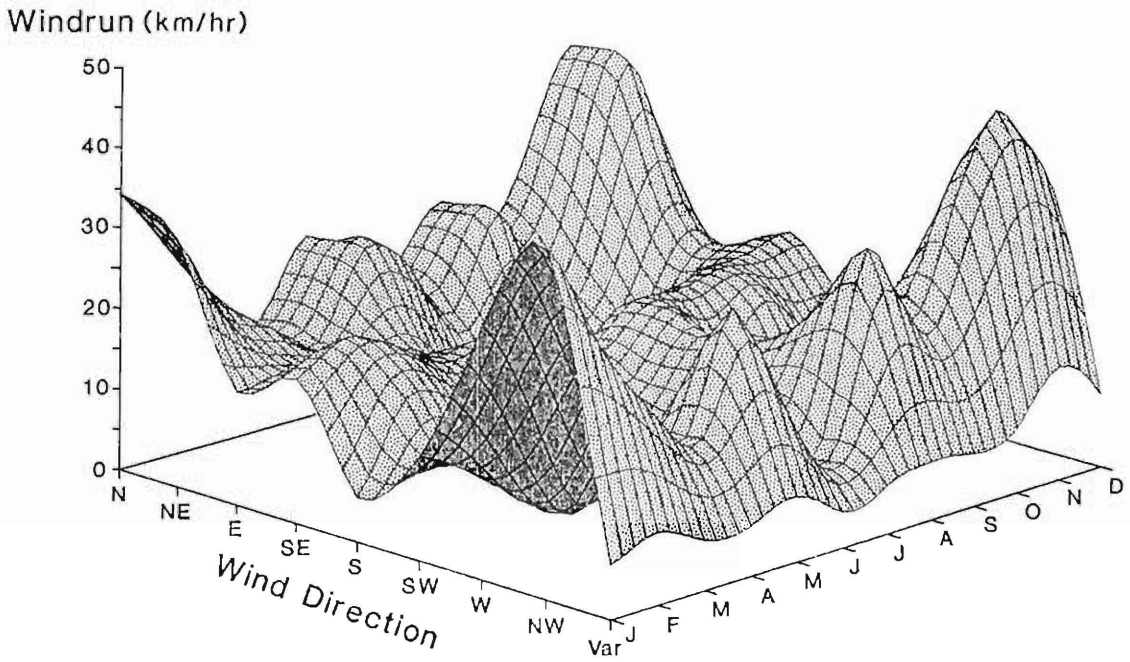


Figure 1.15 Seasonal variation in windspeed at 10m, Puffers Stream 1982. (Var. = Variable wind direction)

(c) Solar Radiation

Incident solar radiation varied from a mean of 6.4 MJ/m^2 day^{-1} near the winter solstice to 26.8 MJ/m^2 day^{-1} during the summer solstice (Fig. 1.16). Clear sky daily maxima ranged from 6.9 to 8.9 MJ/m^2 day^{-1} in winter and from 30.4 to 34.3 MJ/m^2 day^{-1} in summer. The total radiation received in 1982 was ca. 6028 MJ/m^2, though this is only approximate since missing data in July had to be estimated.

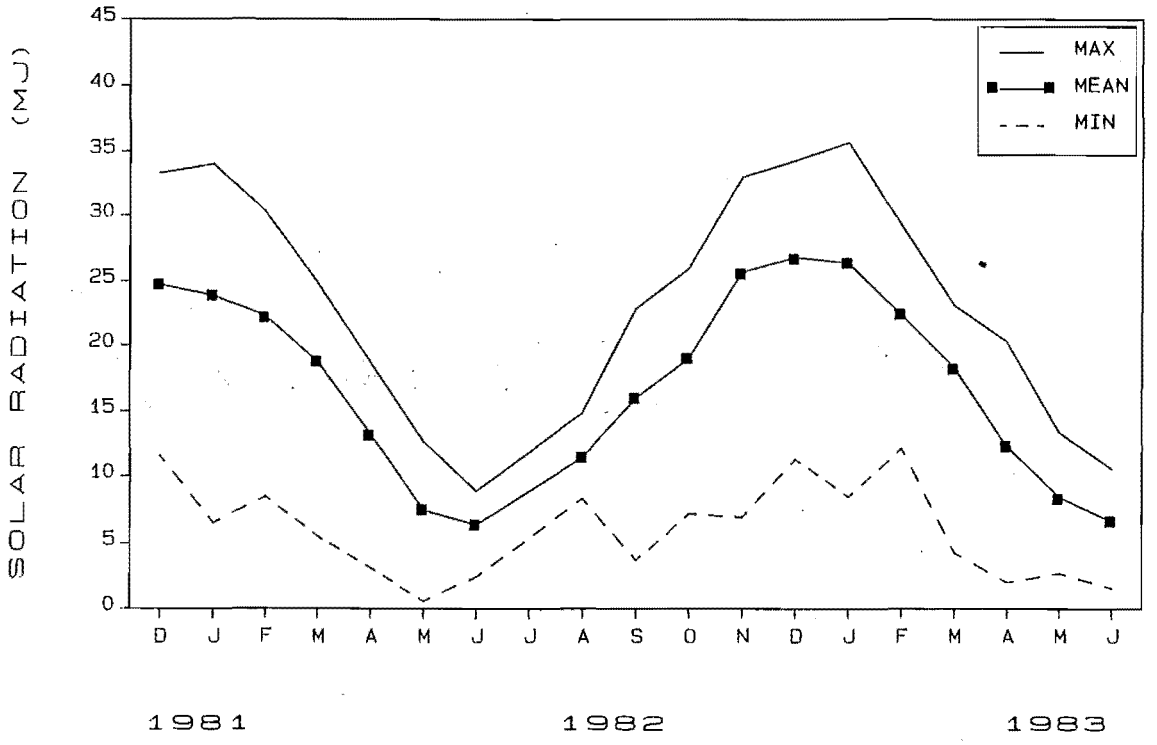


Figure 1.16 Incident solar radiation at Puffers Stream 1982 - 1983.

(d) Temperature

Thermographs accurately record air temperatures during the study. Daily maxima and minima recorded on a Lambrecht themograph from May to October 1981 (n=134) were almost identical to the main Otakeiki thermohygrograph:

Lam Min	(^{0}C)	= -0.28 + 0.99 Otakeiki Min.	(r = 0.993)
Lam Max	(^{0}C)	= -0.56 + 0.94 Otakeiki Max.	(r = 0.992)

The small difference is due to imprecision in chart reading. Otakeiki weekly maxima and minima were then checked against standard maximum and minimum thermometers and a Zeal maximum-minimum thermometer from July 1982 to April 1984. The intercepts, regression coefficients and the high coefficients of determination, show there was no significant calibration drift:

Otakeiki Min (^{0}C)	= 0.30 + 0.98	Zeal	Min	(r = 0.985)
Otakeiki Min (^{0}C)	= 0.95 + 1.00	Alcohol	Min	(r = 0.982)
Otakeiki Max (^{0}C)	= -0.51 + 0.97	Zeal	Max	(r = 0.995)
Otakeiki Max (^{0}C)	= -0.94 + 0.98	Mercury	Max	(r = 0.995)

Mean monthly temperatures rose from minima in July (-0.5 °C 1982) to maxima in February (17.9 °C 1982; Fig. 1.17). Monthly means were above 10 °C from November /December to March. Only in July 1982 was the monthly mean below 0 ^{0}C. Mean monthly minima ranged from -5.1 to 11.9 ^{0}C. falling below zero between May to September in 1981 and from June to July in 1982. The highest mean monthly maximum was 23.9 °C (February 1982) and the lowest 4.1 °C (July 1983).

The minimum recorded temperature was -11.0 °C (September 1981) and the maximum 32.0 °C (February 1982). Air frosts occurred in every month except in March 1982 and January and February in all years.

Topsoil (2 cm) temperatures were always warmer than corresponding mean monthly air temperatures (Fig. 1.18). As expected, they were warmer than 10 cm temperatures with the only exception being July 1982 when the soil was frozen. Temperatures at 20 cm were about 2 °C cooler than at 10 cm in summer, the difference narrowing in autumn. If the topsoil was frozen in winter (e.g. June-July 1981) then subsoil temperatures were about 1 °C warmer than the topsoil. Rapid soil reheating occurred in spring, this starting from August to November depending on season.

Temperatures at all depths peaked in February, before heat was rapidly lost in autumn, reaching minima in June and July.

Diurnal variation in soil temperature was greatest near the surface with a maximum range of 22.2 °C (February 1982) and a minimum of 0.2 °C (June 1982). Maximum variation at 10 cm was 14.0 °C and at 20 cm only 5.5 °C. Minimum diurnal variation was 0.0 ^{0}C at both 10 and 20 cm.

Soil extreme minimum temperatures never dropped below zero from November to February between 1981-1983. In 1981 temperatures at 2 and 10 cm fluctuated below freezing point from March to September but did not pass below ^{0}C at 20 cm. In 1982 freeze-thaw temperatures cycles occurred at 2 cm from April to October whereas at 10 cm this only occurred later, from May to August. At 20 cm, temperatures fluctuated below freezing-point from July to August. A similar pattern occurred in 1983 except that temperatures at 2 cm fell below zero in March but not in April.

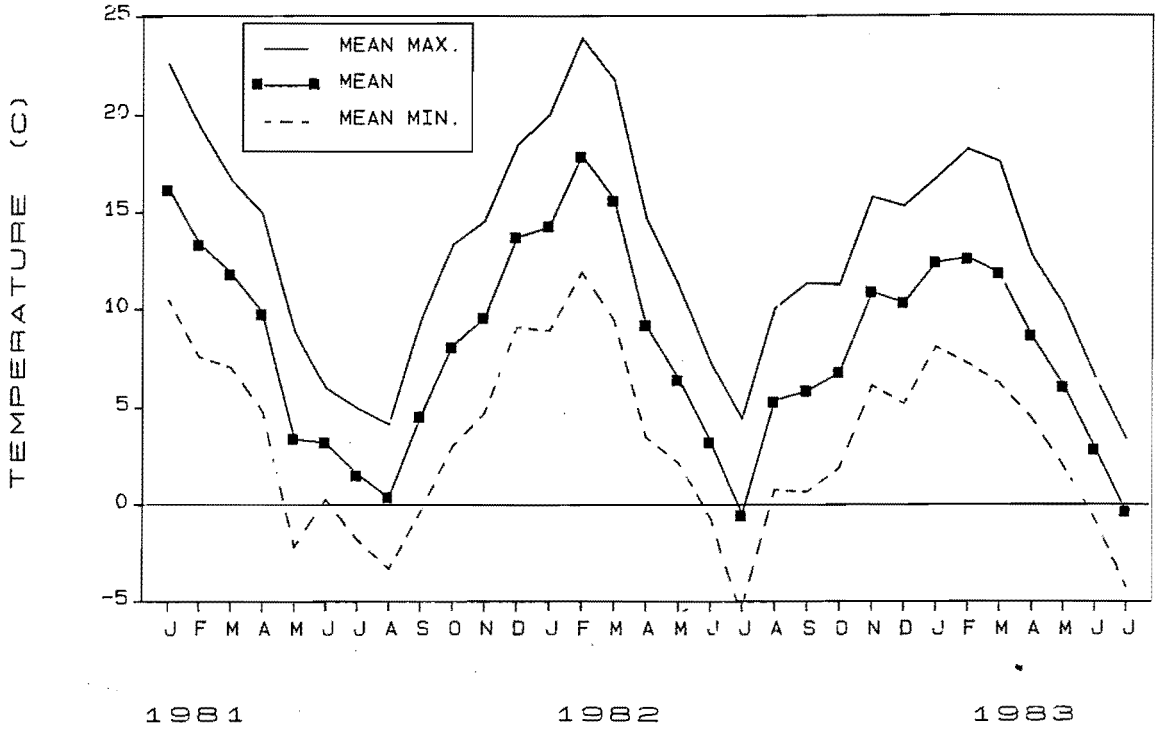


Figure 1.17 Seasonal variation in Screen air temperature 1981 - 1983.

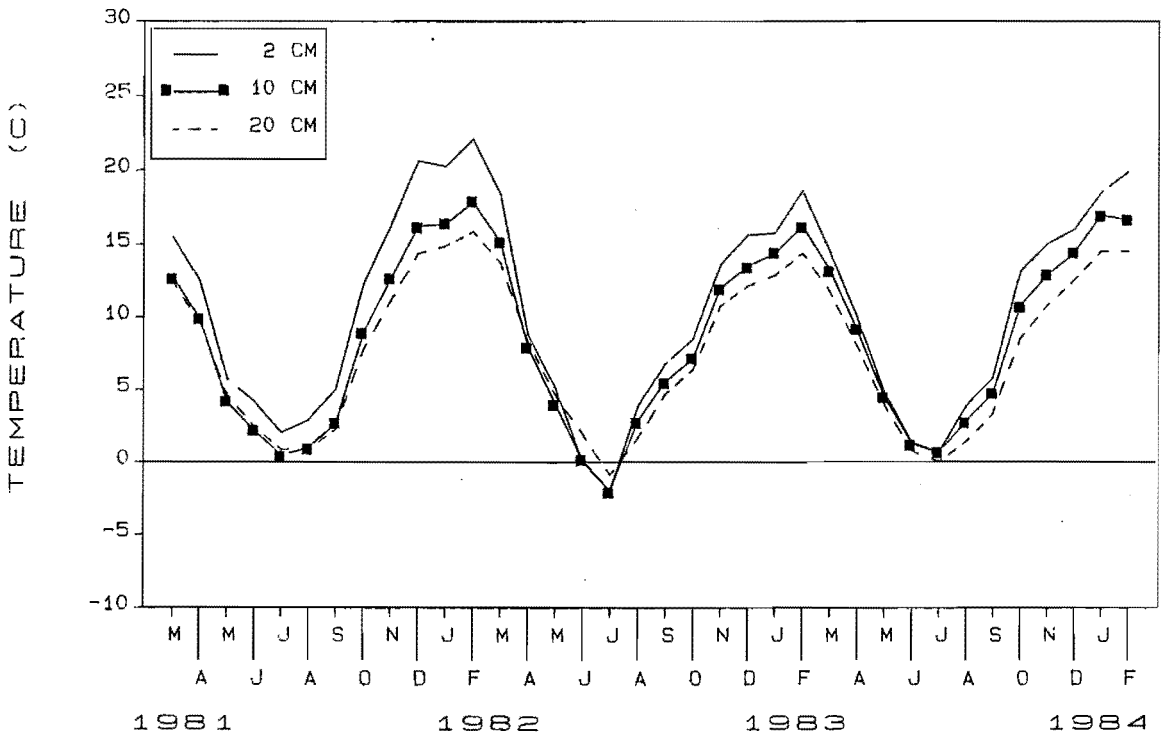


Figure 1.18 Seasonal variation in soil temperatures at 2, 10 and 20cm 1981 - 1984.

1.3.2.3 Discussion

(a) Precipitation

1981 and 1982 were slightly drier and 1983 markedly wetter than normal compared against 16 year means at adjacent stations (Table 1.4).

Table 1.4 Annual Rainfall as Percentage of Mean Annual Precipitation 1964 - 1980

Station	1981	1982	1983
Cass	97.7	97.6	140.8
Craigieburn Forest	99.6	95.9	140.1

The period for which detailed records are available for adjacent stations (1964 - 1980) was slightly drier than the long term normal. Precipitation at the University of Canterbury Cass Field Station, 1964 - 1980 (Sturman and Soons 1984) was 94.1% of the 55 year mean (1920 - 1975, Greenland 1977). However, caution is required in using the Field Station data because of irregularity in collection (Greenland 1977). Correlation of mean annual precipitation 1965 - 1974 with an independent gauge in the Chilton Valley 1.5km away was poor (r = 0.897), almost certainly due to errors in the field station data.

Monthly precipitation at Avoca was most closely correlated with the Chilton Valley, Cass, the nearest station, but also showed high correlation with other mid Waimakariri stations (Table 1.5)

Table 1.5 Correlation of monthly precipitation mid-Waimakariri Basin 1981 - 1983

Station	Avoca	Cass	Mt White	C.Forest	Castle Hill
Altitude (m)	594	610	610	914	741
Mean Annual Pptn (mm).	905	1272	1026	1470	913
Correlation w. Avoca (r)	-	0.94	0.89	0.90	0.88
Period	1981-3	'65-80	'23-80	'64-80	'48-80

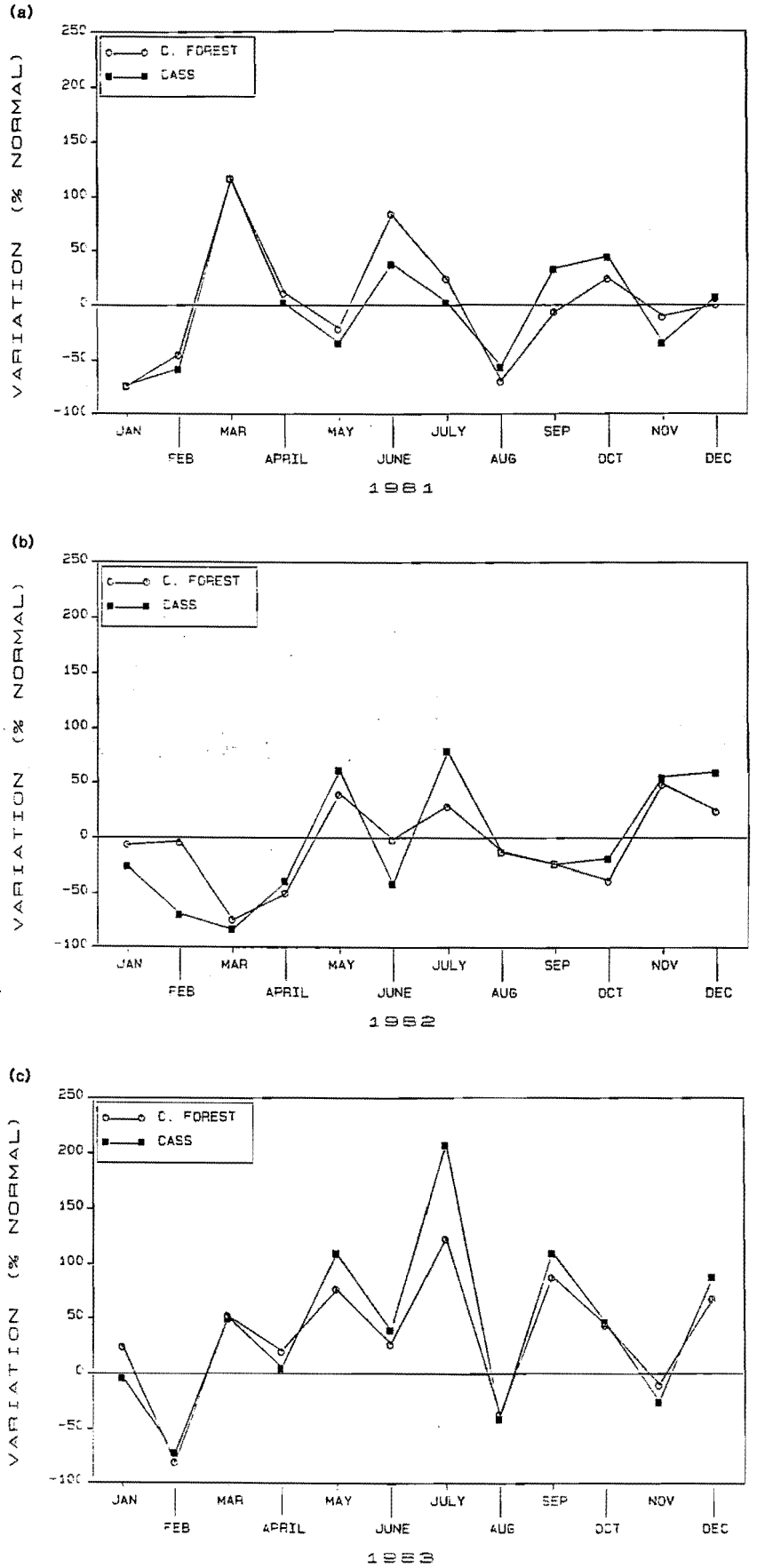


Figure 1.19 Seasonal variation from long-term mean precipitation, 1981 - 1983.

Weekly precipitation, as expected, was also very closely related to adjacent stations (n = 132):

PPN AVOCA	=	1.400	+	0.611 CASS	(r = 0.975)
PPN AVOCA	=	0.975	+	0.531 C.FOREST	(r = 0.958)

Monthly variation from the 16 year means is shown for Cass and Craigieburn for 1981-1983 in Fig. 1.19. Similar variation from the long term means may be inferred at Avoca because precipitation is closely correlated with these stations.

Precipitation recorded at Avoca, approximately half to two thirds that of Craigieburn Forest and Cass, shows the area to be drier than previously mapped, though consistent with the established pattern of rainfall gradients in the basin (Hayward 1967, North Canterbury Catchment Board 1986, Sturman and Soons 1984). The monthly patterns, though variable, are in general accord with previous studies (Greenland and Owens 1967, Sturman and Soons 1984) showing a summer minimum following a spring peak. This is related to the synoptic circulation pattern. High rainfall is associated with the increased frequency of northwesterly airflow in late winter and spring (Section1.3.2b). Low precipitation occurs in late summer due to settled anticyclonic conditions (Sturman and Soons 1984). The low frequency of high intensity precipitation supports previous results (Soons 1971, Coulter and Hessell 1980, Sturman and Soons 1984). Snow precipitation also supports Soons and Rayner's (1968) observations that snow is usually present for one to several days in winter but seldom persists longer.

(b) Wind

The results from this study show windflow patterns in the main valley system and extend the information available from similar investigations in small subsidiary valleys (Greenland 1973, Sturman 1983).

The major factor determining windflow is the interaction between the gross topography of the basin and the dominant synoptic airflow. The synoptic westerly and southwesterly winds produced by anticyclonic progression across the Tasman Sea (De Lisle 1969) are channeled by the general orientation of the Slovens Creek valley between Mt. St. Bernard, Nomans Land and Tarnmoor. Since the valley is orientated north-south (Fig. 1.1) this results in a predominantly northerly airflow. Similarly, orographic deflection of southerly and southeasterly winds by the Torlesse Range up the Waimakariri gorge and then through the southeasterly orientated Rosa saddle, determines the direction of the southeasterly airflows and also partially accounts for their lower mean velocity.

This is similar to the topographic effect demonstrated by Sturman (1983) in the Chilton valley, Cass, though winds differ considerably in magnitude and direction. However, wind directions recorded in the main valley at Cass are almost identical in frequency to those at Puffers Stream, excepting that the predominant wind is northwesterly (Greenland 1977).

The mean annual wind speed at Cass, 4.9 m/s (cited by Greenland 1977) is also almost identical to the 4.7 m/sec mean velocity recorded at 2m on T5. Both records considerably exceed the 1.3 m/s mean daily wind speed reported at Craigieburn Forest (McCracken 1980). Two reasons account for this. Firstly, Craigieburn is topographically sheltered from the main northwesterly flows and secondly, the anemometer was partially sheltered by the surrounding Beech forest (T. McSaveney, pers. com.). This also explains why the percentage of calm or variable winds is far lower at Puffers Stream than the 20% recorded at Craigieburn Forest.

The diurnal variation in wind speed (Fig. 1.12) is closely correlated with thermal effects from incident solar radiation (Sturman 1983). The pattern is almost identical to diurnal variation observed at 1400m in the Craigieburn Range. There the minimum windspeed occurred at 0800hrs and the maximum between 1400 and 1600 hrs (L. Rowe, unpublished data).

Compared with other mountain areas, the average wind speed on T5 at 2m (4.07 m/s) was higher than the 3.1 m/s average recorded at 1257m on the Dogs Range, South Canterbury, at a similar height (Williams 1977). However, it was lower than the five year mean of 7.8 m/s recorded 60cm above ground on the Rock and Pillar Range, at 1390m (Bliss and Mark 1974) or the two year mean of 5.7 m/s recorded at 1.25cm on the Old Man Range (Mark 1965). Winds at comparable latitudes in North American ranges vary from 0.5 to 5.0 m/s (Bliss and Mark 1974).

(c) Solar Radiation

The mean monthly radiation at Avoca in winter is 52.8% of the extra-atmospheric radiation potentially available at 43 ^{0}S. This rises to 63.8% in summer. Peak radiation in winter and summer was 80.6 and 81.8% of the radiation potentially available at the site, almost identical to the 82.0% recorded at Craigieburn Forest (McCracken 1980). However total radiation incident at Avoca was greater than at Craigieburn Forest, though there was an extremely close relationship, as expected, when cloudless day values were compared through the year:

$$\text{AVOCA } (MJ/m^2) = 1.80 + 1.14 \text{ C.FOREST} \qquad (r = 0.995)$$

Comparing all daily radiation values from December 1981 to June 1983, irrespective of diferences in cloud cover, the relationship was still close:

$$\text{AVOCA } (MJ/m^2) = 3.28 + 1.07 \text{ C.FOREST} \qquad (r = 0.995)$$

The mean annual radiation at Avoca, 6028 MJ/m^2 in 1982, was 1.2 times greater than Craigieburn Forest (McCracken 1980) and 1.3 times the mean annual radiation for 1972 on the Dogs Range, South Canterbury (Williams 1977). This is probably largely due to exposure: the Craigieburn Forest site loses up to 12% of the potentially available radiation due to topographic obstruction (McCracken 1980). Williams (1977) also noted topographic obstruction at his Paddle Hill Creek site. However, the change in intercepts,

regression coefficients and the coefficients of determination between the two Craigieburn equations demonstrates a further difference in local solar radiation regimes. The most probable explanation is differential cloud cover. A higher frequency of cloud, due to closer proximity to the Craigieburn range, would lower reception of direct radiation (Coulter 1967, McCracken 1980).

Topographic obstruction explains why the Avoca clear day maxima are only 90% of values recorded on the Rock and Pillar Range, Central Otago (Bliss and Mark 1974). The Rock and Pillar site was located on a broad summit plateau and completely free from obstruction.

Solar radiation levels at Avoca are similar to daily and monthly values in North American Ranges. Daily summer maxima of 30 to 34 MJ m^{-2} are similar to values recorded in the Sierra Nevada (Chabot and Billings 1972, Klikoff 1965), the Olympic and Rocky Mountains and the Northern Cascades (see Billings and Mark 1974), but higher than the foggier Presidential Range (Bliss 1966).

(d) Temperature

The mean annual temperature for 1982 was 8.9 °C, slightly higher than the 8.0 °C long term mean at Craigieburn Forest (McCracken 1980). Mean monthly temperatures, averaged for the whole study, were very closely related to the long term monthly means at Craigieburn Forest (McCracken 1980), the Chilton Valley (1964-68) and the Cass Field Station (1961-64; Greenland 1977):

AVOCA	(^{0}C)	=	- 0.76	+ 1.11	C.FOREST	(r = 0.995)
AVOCA	(^{0}C)	=	- 0.34	+ 0.99	CHILTON V.	(r = 0.990)
AVOCA	(^{0}C)	=	- 0.22	+ 0.92	CASS	(r = 0.976)

The pattern of monthly temperatures at Avoca was also very similar to that recorded on the Dogs Range (Williams 1977) though temperatures were, on average, 2-4 ^{0}C higher. They were considerably higher than the mean air temperatures described for Central Otago by Mark and Bliss (1970) and Bliss and Mark (1974). Not surprisingly, they are also higher than mean temperatures at higher altitudes in North American ranges at generally similar latitudes (40-48°N, Bliss 1966 1969).

Soil isotherms show the same general pattern observed on the Dogs Range (Williams 1977), but are considerably warmer than those reported for the Rock and Pillar range (Bliss and Mark 1974).

1.4 SOILS

1.4.1 General

Soils in the Waimakariri basin have been broadly classified and mapped at a scale of 1:253,400 (Soil Bureau 1967, 1968). Their pedogenesis, morphology and chemistry are reviewed by Vucetich (1969) and Cutler (1977). Studies in the basin and similar areas (McDonald 1961, McCraw 1962, Ives 1970, Leamy 1971, Ives and Cutler 1972, Harvey 1974, Molloy and Blakemore 1974, Campbell 1975, Webb 1976, Harrison 1982, Archer and Cutler 1983, Tonkin 1984, Lynn and Tonkin 1985, Basher 1986, Webb *et al.* 1986, Lynn 1987) enable construction of a conceptual framework by which to understand the main soil sequences and processes (Tonkin *et al.* 1977, Young *et al.* 1977, Basher and Tonkin 1985) although still ".... *many gaps exist in the pedology of this region.* " (Cutler 1977, p 177). This study attempts to narrow one of these gaps by detailed examination of soil fertility in the Craigieburn set.

Craigieburn soils, occurring on terraces and fans, occupy 2.6% of the Catchment (Hayward 1967). Occurring elsewhere from Marlborough to Southland they comprise approximately 0.2% of the soils in the South Island (Long 1966). They are classified as strongly leached, hygrous, high country yellow-brown earths (or eldefulvic soils; N.Z.Genetic Classification, Taylor and Pohlen 1962) or Dystochrepts (Soil Taxonomy, U.S.D.A.,1975). They are one of the few high country soils to be classified as arable, with moderate physical limitation (Land Use Classes III and VI, Howard and Prickett 1967, Ministry of Works 1974, 1979). The major limitation to cultivation is susceptibility to wind erosion.

Results of early agronomic trials on Craigieburn soils are reviewed and summarised by O'Connor (1967). Subsequently, the main edaphic research emphasis in the Waimakariri shifted to steepland soils (Molloy 1964, Wilde 1974, Furkert *et al.* 1975, Young pers. com., Burns *et al.* 1984) particularly the rehabilitation of eroded subsoils (Dunbar 1971, 1974, Nordmeyer and Davis 1977, Nordmeyer *et al.* 1978, Davis 1981 a,b,c). Further research on terrace soils lapsed until Ali (1974) compared the effects of phosphorus and lime on grass and legume growth between potted Craigieburn, Cass and Katrine soils. Kee (1981) examined the P response of three legumes in a field trial on a Craigieburn soil at Cave Stream, terrace CB3.

The pedology and chemistry of a sequence of terrace soils at Cave Stream was investigated by Tonkin (1981), the most intensive study of Craigieburn and related soils to date. However, this study and the previous studies examined Craigieburn soils formed under relatively high rainfall. No published information is available about Craigieburn soils, or their agronomic performance, in the drier rainfall zones in the basin. Hence a soil development sequence, similar to the Cave Stream sequence but formed under lower rainfall, was investigated at Puffers Stream, near Avoca.

1.4.2 Methods

At Puffers Stream, five soil profiles were exposed on each surface. Pits were systematically placed in each quarter of the lower two terraces with the fifth in the centre. Pits were placed 10 - 15 m apart on a transect parallel to the Stream on the third and fifth terrace. The second and fourth pits were indented about 10 m. The same pattern was used on the fourth terrace except pits were 80 - 100 m apart. Pedological procedure and description followed Taylor and Pohlen (1962) except for horizon designations which follow FAO (1974) terminology. Samples at three depths (5-10cm, 20-30cm, 40-45cm) were removed from each profile for chemical analysis. Twenty 0-10cm topsoil samples were bulked for each surface and used for Ministry of Agriculture and Fisheries (MAF) quick test assays (Mountier *et al.* 1966). Five additional profiles on the main terrace, T4, were described but not sampled.

Samples were air dried, passed through a 2mm sieve and analysed for pH in distilled water, pH in 0.01m KCl, sodium fluoride reactivity, phosphate retention, and 1.0 normal H_2SO_4 extractable phosphorus using standard procedures (Blakemore *et al.* 1981)

After initial investigations were completed, a representative pit on each terrace (ca 1m x 1m x 1.5m) was excavated for description and sampling by 10cm depth increments.

1.4.3 Results

Profile variability on each terrace is shown in Fig. 1.20 and summarised in Fig. 1.21. Soil quick test results are given in Table 1.6 and exploratory chemical analyses summarised in Table 1.7. Descriptions of a representative profile for each terrace follow.

Table 1.6 Topsoil Quick Tests T1 - T5

TERRACE	pH(H_2O) 1:2.5	pH(KCL) 1:2:5	pH(NaF) 1:50 5 min.	Cations Ca	Mg	K	Mg-HCL	Olsen P	Bray 2 P	$S\text{-}SO_4$	Total N %	P Retension %
T1	5.7	4.35	7.90	6	34	10	2500+	8	8	4	.29	24
T2	5.4	4.15	9.20	3	19	12	2500+	15	13	3	.28	52
T3	5.3	4.10	9.80	1	5	3	2500+	7	8	4	.33	41
T4	5.4	4.10	9.00	2	14	10	2500+	6	5	4	.27	50
T5	5.2	3.80	7.60	2	15	6	2500+	6	2	3	.22	37

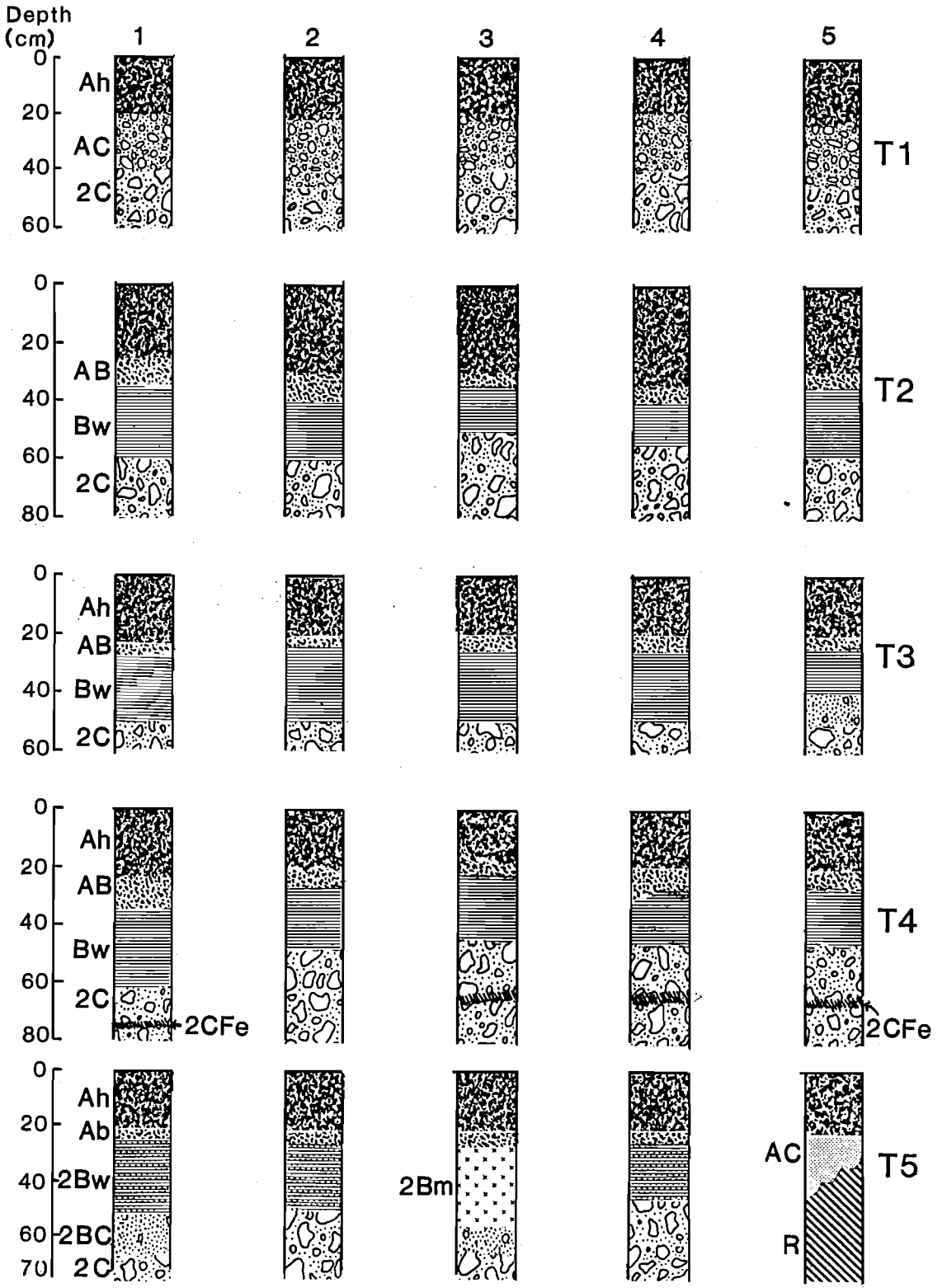


Figure 1.20 Profile variability in Puffers Stream Terraces T1 - T5.

Table 1.7 Initial soil chemical analyses T1 - T5

Terrace and Horizon depth (cm)	pH (H_2O) 1:2.5	pH (KCl) 1:2.5	Δ pH	pH (NaF) 1:50	Phosphorus Retention %
T1 5-10	6.1	4.4	1.7	10.1	25
20-30	6.4	4.5	1.9	10.3	19
40-45	6.5	4.5	2.1	10.3	18
T2 5-10	5.9	4.2	1.6	10.1	46
20-30	6.0	4.3	1.7	10.3	59
40-45	6.1	4.5	1.6	10.6	69
T3 5-10	5.6	4.2	1.4	10.2	53
20-30	5.8	4.3	1.4	10.6	75
40-45	5.9	4.7	1.2	10.8	76
T4 5-10	5.8	4.2	1.4	10.2	46
20-30	6.0	4.3	1.7	10.4	64
40-50	6.2	4.7	2.1	10.6	59
T5 5-10	5.7	4.0	1.6	10.0	23
20-30	5.7	3.9	1.8	10.0	34
40-45	6.1	4.3	1.8	10.3	55
ANOVA 5-10	***	***	ns	***	***
20-30	***	***	***	***	***
40-45	***	***	***	***	***
C.V. % 5-10	2.1	1.7	9.1	1.0	10
20-30	1.7	1.6	7.0	1.0	12
40-45	2.5	3.6	12.3	1.6	17

where ANOVA = Analysis of variance

C.V. % = Coefficient of variation %

ns = Probability level not significant

*** = Probability level $p < 0.001$.

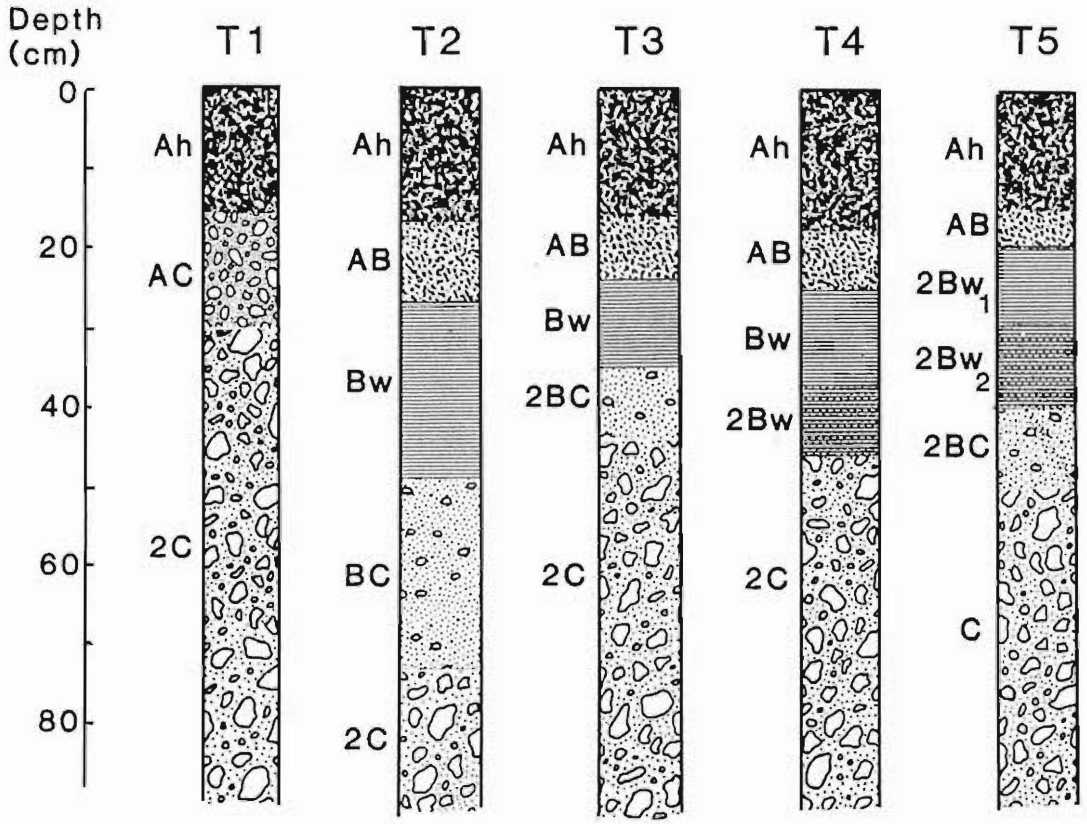


Figure 1.21 Modal profile morphology T1 - T5.

Terrace One

Site: *Festuca novae-zelandiae* grassland and *Discaria scrub*; flat; well drained.

Depth (cm)	Horizon	Morphology (Plate 7)
0 - 5	Ah.1	10YR 3/2 very dark greyish brown; fine sandy loam; moderately developed fine granular structure with crumbs; friable; abundant fine roots.
5 - 16	Ah.2	10YR 3/2 very dark greyish brown; fine sandy loam; weakly developed fine granular structure with crumbs; friable; abundant fine roots.
16 - 30	A/C	10YR 3/3 dark brown; loamy sand,very stony, medium to large weakly weathered rounded boulders; loose; many fine roots.
30 - 100+	2C	2.5YR 3/2 very dark greyish brown, gravels with stones and occasional boulders, rounded, weakly weathered loose, single grained; few fine roots.

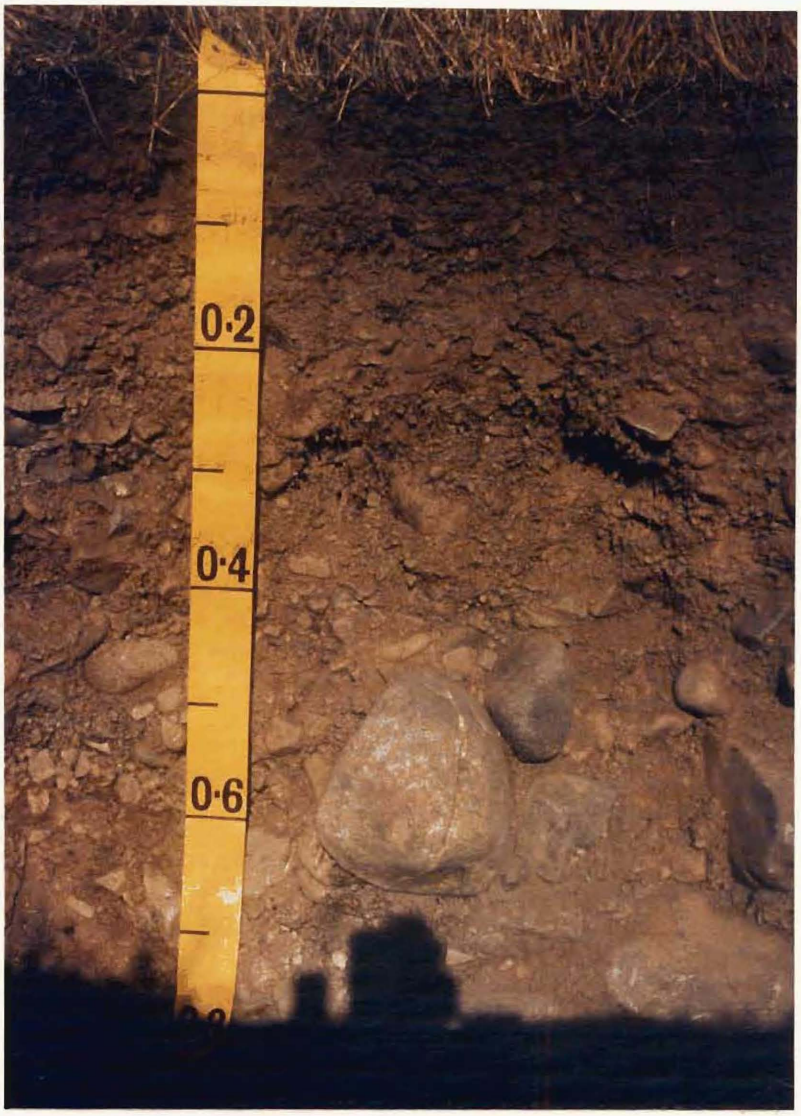


Plate 7 Recent soil, Terrace 1

Terrace Two

Site: *Festuca novae-zelandiae* grassland; flat; well drained.

Depth (cm)	Horizon	Morphology (Plate 8)
0 - 6	Ah.1	10YR 2/2 very dark brown; silt loam, stony, subangular, weakly weathered and some pitted stones; moderately developed fine to very fine granular structure with some fine crumbs; friable; abundant fine and few medium roots
6 - 17	Ah.2	10YR 3/2 very dark greyish brown; silt loam with stones, subangular weakly weathered; moderately to strongly developed fine to very fine nuts, few medium nuts and fine crumbs; abundant fine and few medium roots
17 - 27	AB	10YR 3/2 very dark greyish brown to 10YR 5/5 yellowish brown; silt loam with subangular,weakly weathered stones; strongly developed fine to very fine nutty structure with some medium nuts and fine crumbs; friable; many fine and few medium roots; distinct wavy boundary.
27 - 49	Bw	10YR 5/5 yellowish brown; silt loom with gravel and weakly weathered sub-angular stones; very weakly developed medium blocky structure to massive, slightly coherent single grained; few fine roots, distinct smooth boundary.
49 - 73	BC	10YR 4.5/4 dark yellowish brown; gravelly sand with sub-angular weakly weathered stones; loose; massive, non-coherent; few fine roots; distinct smooth boundary.
73 - 110+	2C	10YR 3/3 dark brown; gravels and sub-angular, weakly weathered stones; loose; single grained, non-coherent; v.few roots.

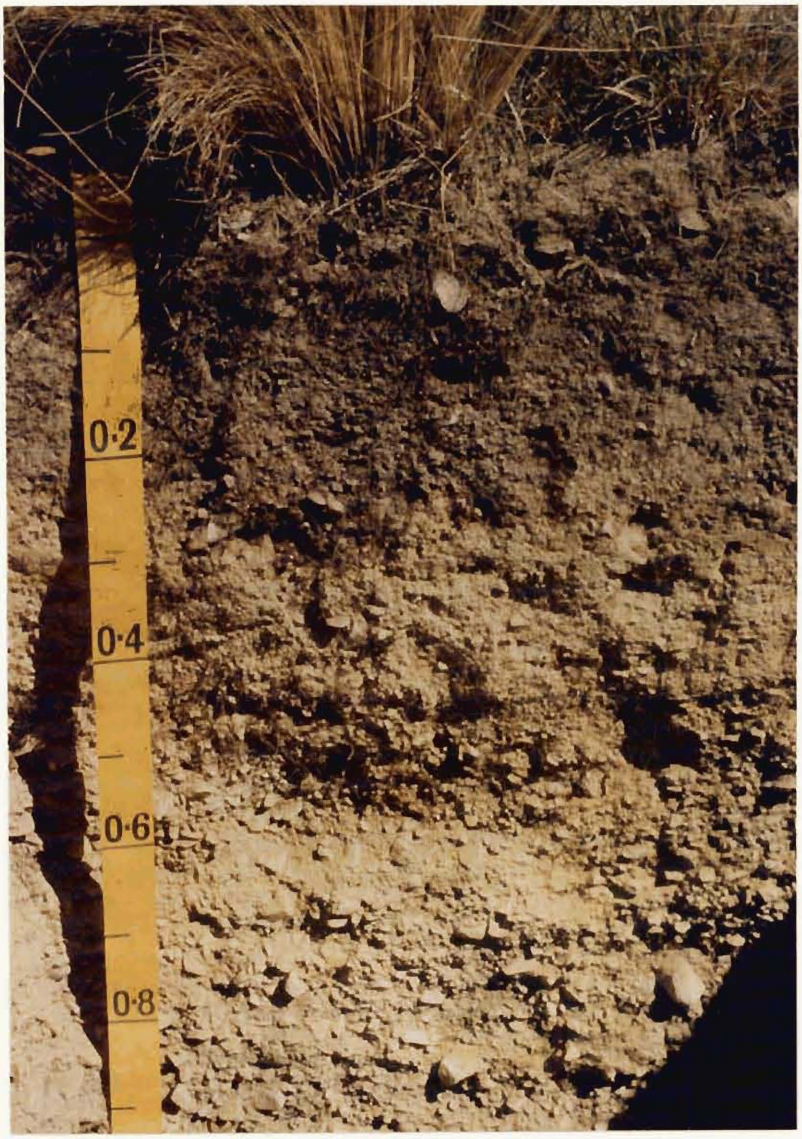


Plate 8 Young yellow-brown earth soil, Terrace 2

TERRACE THREE

Site: *Festuca novae-zelandiae* grassland; flat; well drained.

Depth (cm)	Horizon	Morphology (Plate 9)
0 - 8	Ah.1	9YR 3/2 very dark greyish brown; silt loam with sub-angular weakly weathered stones; moderately to well developed composite medium to fine granular and fine to very fine crumb structure with some fine nuts; friable, peds firm; abundant fine and few medium roots; distinct boundary.
8 - 10	Ah.2	10YR 3/3 dark brown; silt loam with few sub-angular weakly weathered stones; well developed medium and fine nutty with some fine to very fine crumb granular structure; friable to firm; many fine roots; indistinct boundary.
16 - 24	Ah.2/Bw	10R 3/3 dark brown and 10 YR 5/7 yellowish brown; silt loam with few angular weakly weathered stones; moderately developed medium to fine nutty structure friable; few medium, and fine roots; distinct boundary.
24 - 35	Bw	10YR 5/7 yellowish brown; silt loam with sub-angular weakly weathered stones; well developed fine nutty structure; friable; few medium roots; distinct boundary.
35 - 43	2BC	10YR 5/3-4 brown to yellowish brown; silt loam with gravel; stony, sub-angular weakly weathered stones; very weakly developed fine nutty structure, almost massive; many roots; sharp boundary.
43 - 120+	2C	2YR 4/3 dark greyish brown to olive brown; unconsolidated gravels and sub angular weakly weathered stones, very stony; loose, single grained; a few fine roots.

Plate 9 High-country yellow-brown earth soil, Terrace 3

TERRACE FOUR

Site: *Festuca novae-zelandiae* grassland; flat; well drained.

Depth (cm)	Horizon	Morphology (Plate 10)
0 - 9	Ah.1	10YR 2/3 very dark brown; silt loam stones with a few surface boulders, weakly weathered to pitted; abundant fine, few medium roots; friable, firm to extremely firm peds; strongly developed medium to fine granular structure with some crumbs; abundant fine and medium roots; distinct boundary.
9 - 18	Ah.2	10YR 3/2 very dark greyish brown; wilt loam with few weakly weathered rounded stones; friable, firm to extremely firm peds]; moderately developed medium nutty structure with few fine granules and coarse worm cases; many fine and medium roots; indistinct boundary.
10 - 25	AB	10YR 3/2 very dark greyish brown and 10YR 5/6 yellowish brown; silt loam with few weakly weathered rounded stones; friable to firm; moderately developed medium to coarse nutty structure with some fine nuts; few roots; distinct boundary.
25 - 38	Bw	10YR 5/6 yellowish brown, silt loam with few weakly weathered rounded stones; very firm; weakly developed fine to medium blocky structures; few roots; distinct boundary.
38 - 46	2Bw	10YR 5/4-5 yellowish brown; sandy loam with few weakly weathered rounded stones; firm; very weakly developed platy structure; very few roots; clear boundary.
46 - 100cm+	2C	10YR 5/3-5 brown to yellowish brown; loamy sand to gravelly sand, stony, weakly weathered rounded stones; friable-firm; v. weakly developed platy structure to massive, single grained, incoherent; iron accumulation and staining 70-75 cm; very few roots.

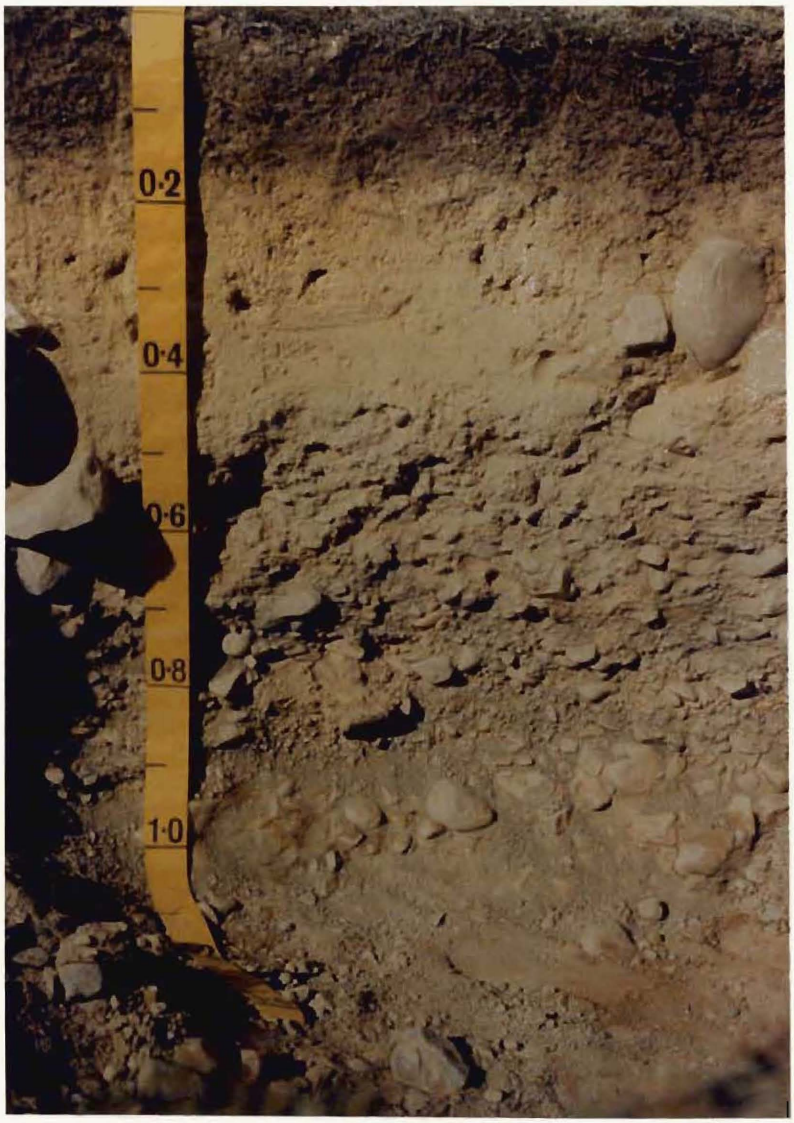


Plate 10 High-country yellow-brown earth soil, Terrace 4.

TERRACE FIVE

Site: *Festuca novae-zelandiae* grassland; gently sloping; well drained.

Depth (cm)	Horizon	Morphology (Plate 11)
0 - 5	Ah.1	7.5YR 3/2 dark brown; silt loam with pitted stones, rounded, friable; strongly developed composite fine to coarse granular structure with a few fine crumbs; abundant fine and medium, few coarse roots; indistinct boundary.
5 - 15	Ah.2	10YR 3.5/3 dark brown; silt loam with boulders and some weakly weathered rounded stones; firm, peds very to extremely firm, well developed many fine to few medium nuts with fine granules; many fine, few medium roots; large worm casts; indistinct boundary.
15 - 20	AB	1YR 3.5/3 to 10YR 6/5 mixed dark to yellowish brown; silt loam with clay; occasional weakly weathered rounded stones; moderately firm to firm; peds very to extremely firm; many fine few medium roots; indistinct boundary.
20 - 30	2Bw.1	10YR 6/5 light yellowish brown; silt loam with clay; few weakly weathered rounded stones; very to extremely firm; moderately to strongly developed medium blocky structure, faces of peds organic? coated; few fine roots; distinct boundary.
30 - 40	2Bw.2	10YR 5/6 yellowish brown; silt loam with sand; few weakly weathered rounded stones; firm, crumbling to a friable powder; weakly developed fine to medium blocky structure; very few fine roots; distinct boundary.
40 - 50	2BC	10YR 5/5 yellowish brown; sand loam with stones; friable to firm; massive, slightly to moderately coherent (incipient platy structure); very few roots; sharp boundary.
50 - 120+	C	2.5YR 5/3 greyish brown; loamy sand with stones and occasional boulders; extremely firm; massive, moderately coherent; structureless.

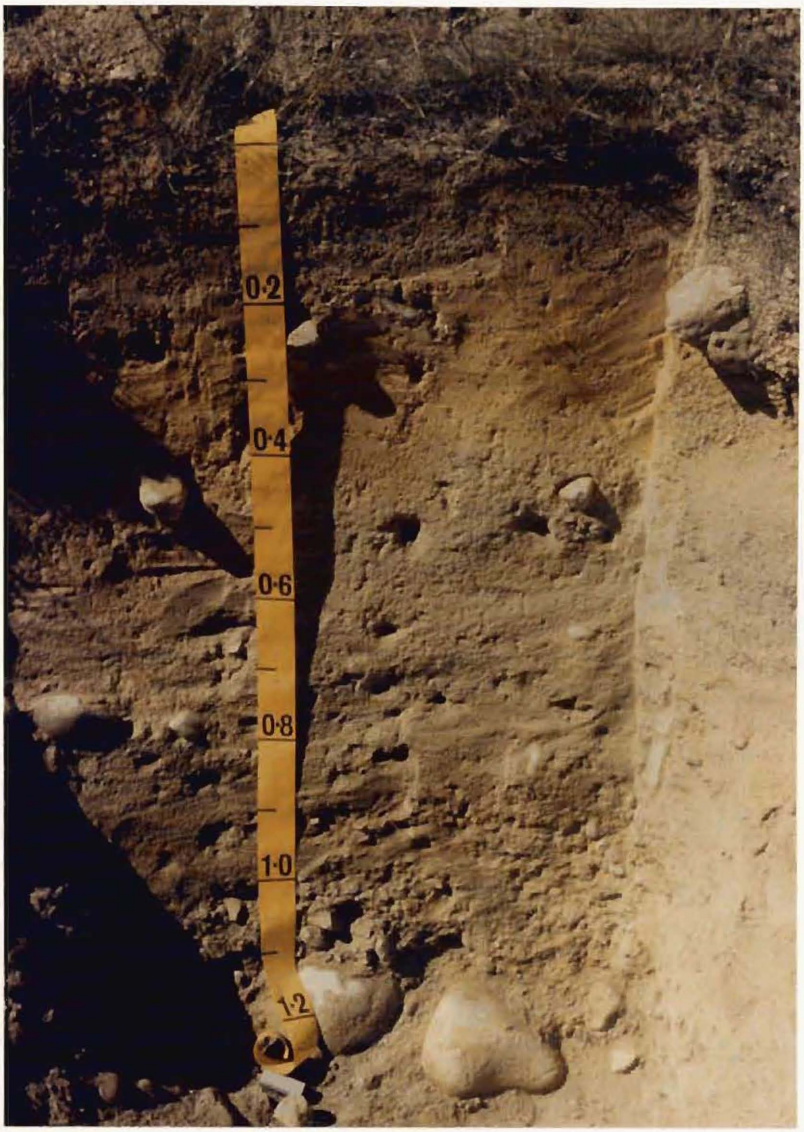


Plate 11 High-country Yellow-brown earth soil, Terrace 5

1.4.4 Discussion

The initial pedological and soil chemical investigations showed highly significant differences between terraces (Table 1.7; Fig. 1.20). The trends in properties are consistent with pedological development of the soils in the order T1 < T2 < T3 ≤ T4 < T5. Soil pH, for example, is highest on T1 and decreases on subsequent soils. T5 has the lowest pH(KCl) values, indicative of greater development relative to the other soils (Walker and Stevens 1970). The absence of B horizon development shows T1 is considerably younger than the remaining soils.

Fluoride reactivity and phosphorus (P) retention are good indices of soil development (Fieldes and Perrott 1966). They are closely related to the quantity of short range order (amorphous) aluminosilicates present (Saunders 1965). Thus fluoride reactivity increases from T1 to T3 and then drops on T5. P retention follows a similar pattern. The low values in T1 and their highest occurrence in the Ah horizon are again indicative of a young soil. The increase in values in T2 to T4, and peak values occurring in subsoils, demonstrates progressively greater weathering and mobilisation of aluminium, probably in the form of proto-imogilite (Farmer *et al.* 1980). The decrease in fluoride reactivity and P retention again differentiates T5 from lower terraces and is probably associated with formation of secondary, pedogenic clays.

Profile variability on each terrace is small with the exception of T5. On the lower terraces depth to C horizon gravels and the thickness of the AB horizon were the most obvious differences (Fig. 1.21). Aeolian truncation of profiles is indicated by the higher surface stone contents of T3, T4 and possibly T5 (Section 1.5.3). Assuming loess deposition was similar on the main outwash surfaces of Cave and Puffers Streams, and further assuming minimal erosion before burial, the 60cm loess column in the Cave Stream paleosol C5 (Tonkin 1981) suggests approximately 20cm of loess may have been removed from soils currently at the surface in both sites.

The variability on T5 is related to parent material. Soils developed on glacio-fluvial deposits on the northern and eastern sections of the surface have brown Ah horizons (7.5 YR 4/2) and yellow brown subsoils (7.5 YR 5/4 to 4/6; Fig. 1.21; pits T5.1, T5.2). Profile colours progressively redden westward towards the basaltic intrusive rock exposed at the edge of the scarp. Top and subsoil colours directly above the rock (Fig. 1.21; pit T5.5) are dark red brown (2.5 YR 3/3). The other interesting variant is the perched gley horizon in flat sites due to impeded drainage caused by the compacted C horizon subsoils. Abundant fine to medium mottles (5 YR 4/6) are indicative of seasonal fluctuations in the water-table. These differences were not investigated further. The experimental plot and representative profile were located on free draining soils developed in fluvio-glacial greywacke parent material.

Charcoal was found only on T5. Here it was scattered in discrete fragments throughout AB horizons and, to a lesser extent, B horizons. Evidence such as windthrow dimples and sinusoidal undulating B horizons near the surface (visible on the Flock Hill road (Grid Reference: S66 316 035) strongly suggests with botanical evidence

(Section 1.5), a previous forest on these soils. There was insufficient charcoal to date but it may date from one of the major fires 500 - 600 years B.P. (Burrows 1983) or possibly a more recent event.

Why no charcoal was found on the lower terraces is enigmatic. Possibly the charcoal on T5 derives from scrub restricted to T5 but absent from lower surfaces.

Precise dating of the soils is not possible. The maximum geological age for the oldest surface, T5, is ca. 24,000 years and ca. 18,000 years for T4 (Gage 1958). Soils are incontestably younger than this from stone weathering rinds. If Tonkin's (1981) dating for loess inception is correct and if, as seems reasonable, loess deposition at the two sites was synchronous, then the maximum age for the loessial 2Bw horizon in T5 will be in the order of 7,000 years. The soil on T4 may be a younger variant, or may be on younger loess. Following Cutler's (1977) schema it probably dates about 3,000+ years. T3 and T2 probably fall within 1,000 - 3,000 and T1 somewhere around 300 years.

Soil chemical properties (Tables 1.6, 1.7) are within the range characteristic of moderately to strongly leached high country yellow brown earths (Soil Bureau 1968, Cutler 1977). Topsoil pH values are rated as moderately acid (medium) on T1 (Blakemore *et al.* 1981) and vary between low to moderately acid on the remaining surfaces. Topsoil P retention was low in T1 and also in T5 but was medium in all other topsoils (Blakemore *et al.* 1981). Subsoils in T1 and T5 only had moderate P retention whereas high P retention occurred in T2 - T4 subsoils, except in the 20 - 30 cm horizon where values just fall short of the 'high' class.

Calcium values are medium in T1 and low in the older topsoils T2 - T5. All soils had medium to high magnesium and potassium levels except T3 which is low. Phosphorus levels were low, well below the critical limit of 12 ppm, in all soils except T2. Sulphur values are low in all topsoils but plant-available sulphate is likely to be present in subsoils. Nitrogen levels are medium in all topsoils.

The profile morphology of mature Puffers Stream soils is generally similar to other soils classed in the Craigieburn set, yet there are some striking differences. Topsoils at Puffers Stream have moderately to strongly developed nut structure in comparison to the predominant, strongly developed fine and medium crumb structure found in comparable Ah horizons in Craigieburn soils under higher rainfall (eg. Cave Stream, Tonkin 1981). Subsoil bulk densities are significantly higher at Puffers Stream (Section 8.3).

The large native worms, *Oligochaetus* spp. are present at Puffers Stream at a density of 1.4 worms m^{-2} $10cm^{-1}$ depth, but totally absent, or present at a much lower frequency, at Cave Stream. This may explain the nut structures: they may be direct derivations from worm casts.

The difference also shows in soil chemistry. Fluoride reactivity and P retention values are higher at comparable Cave Stream soils. For example, P retention in Cave Stream CB4, Ah and Bw horizons were 72% and 82% compared with 47% and 64% for

similar horizons on T4 at Puffers Stream. It is evident these soils are sufficiently different to warrant taxonomic separation.

After the preliminary investigations, discussed above, the chemistry and mineralogy of the sequence were intensively investigated using 10 cm depth samples of the representative profiles (Harrison and Swift 1984).

The distribution and soil/landform relationships of these terrace and related soils on Flock Hill are currently being investigated as a model of the montane eastern South Island (Lynn and Tonkin 1985, Lynn 1987).

1.5 VEGETATION

1.5.1 General History

The framework of the late Otiran and Aranuian vegetation history in the Waimakariri has been successfully reconstructed by pollen analysis and radiocarbon dating. The principal study sites are all reasonably close to the Study Area and results can be extrapolated with confidence:-

Site	Distance from Study Area	Reference
Kettlehole Bog	12 km NW of Avoca	Lintott 1963
"		Moar 1966
"		Lintott and Burrows 1973
"		Burrows 1983
Lake Hawdon	7 km N of Avoca	Moar 1971
Vagabond Inn	2 km E of Avoca	Moar 1971
Mt. Horrible Mire	12 km N of Cave Stream.	Moar 1971
Woolshed Hill	16 km N of Cave Stream.	Moar 1971
Lyndon Stream	25 km SW of Cave Stream.	Moar 1980

Grassland dominated the late Otiran landscape in the Central South Island from ca 26,000 yrs. to about 12,000 yrs. B.P. (Moar 1980). Gramineae and Cyperaceae were the major components with restricted areas of shrubs, principally *Phyllocladus, Coprosma, Dracophyllum* and *Myrsine*. Some isolated *Nothofagus* forest survived in refugia (Wardle 1963,Lintott and Burrows 1973). Vegetation cover was relatively sparse (Lintott and Burrows 1973) and almost certainly discontinuous in montane sites such as the Waimakariri. Climatic conditions were bleak with probably a colder, drier climate than present (Moar,1980). Chinn (1976) estimates the average temperature during the Otiran to be 3.8 °C cooler than present.

The open grassland and scrub mosaics were replaced by shrubland in the early Aranuian when climatic conditions improved. The sequence appears to have been first, *Halocarpus bidwillii* scrub, then *Phyllocladus asplenifolius* var *alpinus* and other shrubs eg. *Hebe* and *Pseudopanax* (Moar and Lintott 1977). *Podocarpus hallii* forest began to spread about 10,000 yrs. ago until it dominated the upper Waimakariri about 7,500 yrs.

B.P. (Burrows 1977). Continuing climatic improvement assisted the spread of Podocarps. *Dacrycarpus dacrydioides, Prumnopitys taxifolia* and *Prumnopitys ferrunginea* invaded, but did not replace, the *Phyllocladus* shrubland. Precisely when this occurred is uncertain, but Moar (1971) considers it began before 8,000 yrs. B.P.. Later, sometime before 6,600 yrs. B.P. *Nothofagus* forest began to spread in the basin and replace the mixed Podocarp mosaic (Burrows 1983).

Mountain beech, *N. solandri* var *cliffortioides* then became dominant over large areas until its widespread destruction by fire, attributed to Polynesian burning (Molloy, *et al.* 1963, Molloy 1964, 1969, 1977, McGlone 1983). Fire frequency in Canterbury increased by an order of magnitude from 1,000 to 500 yrs. B.P., with the greatest frequency between 550 - 500 yrs. B.P. (McSaveney and Whitehouse, in press), but the actual number of Polynesian fires is unknown. Molloy (1977) published ^{14}C charcoal dates ranging between 786 ± 53 to 392 ± 37 yrs. B.P. It appears that forest removal may not have been synchronous throughout the region. The charcoal and pollen evidence near Porters Pass suggests a fire about 750 yrs. B.P. (McGlone 1983). A similar investigation at Kettlehole bog showed that a major fire occurred at 531 ± 57 yrs. B.P. (Burrows 1983). Burrows argues that this particular fire was responsible for widespread deforestation throughout the Waimakariri. Natural fires are known to have occurred earlier and may also have resulted in earlier deforestation (Molloy 1977, Burrows 1983).

Following the removal of forest, short grassland developed, largely from riparian sources (Cockayne 1928). The tall tussocks, *Chionochloa macra, C. rigida* and *C.flavescens*, later migrated downslope from the alpine zone, eventually forming a continuous tall tussock grassland (Connor 1964, Connor and Macrae 1969). Red tussock, *C.rubra*, would also have expanded into adjacent sites. Connor tentatively suggests that 200 years elapsed or less, depending on site factors, before a close-canopied tall tussock grassland established.

European burning and grazing, as is well known, transformed tall tussock grasslands into short tussock grasslands with fescue tussock, *Festuca novae-zelandiae* the principal species (Connor 1964, 1965). Reviewing the effects of European pastoralism on tussock grasslands, O'Connor (1982, 1986) emphasises the rapidity of the change: by the 1880's the gross transformation was largely complete. Burrows (1977), discussing the history of the Waimakariri grasslands, concluded that there were '*enormous changes*' but '*... there is no precise knowledge of how much, or in what ways, the proportion of the native components have been influenced by burning and grazing...*'.

While the range of species found today is probably similar to that found before European settlement, their relative abundance and possibly intra-specific composition, almost certainly is not (O'Connor 1986). The main changes are the selection under grazing for less palatable plants and invasion of exotic species, particularly *Agrostis tenuis* and *Anthoxanthum odoratum* (see Cockayne and Foweraker 1916, Malcolm 1925, Sewell 1947, O'Connor 1986). Dobson (1977) summarises what is known about the adventive flora in the area.

1.5.2 Vegetation at Puffers Stream

1.5.2.1 Methods

(a) Species Area Relationships

Quadrats of geometrically increasing size, 25cm, 50cm, 1m, 2m, 4m, 8m and 16m square (Goodall 1952, Kershaw 1973) were carefully examined to determine the vascular species present in fescue tussock grassland on T4. Three separate areas were examined. A single 50m square quadrat was also assessed.

(b) Floristic Description

A 10m x 10m plot (Connor 1961, 1964, 1965, Kershaw 1985) was randomly located on each surface using a 100m tape. The tape was orientated north-south, parallel to Puffers Stream with the starting point being positioned in subjectively chosen grassland. Limited area on the first terrace necessitated using a 30m tape, orientated east-west. The origin of each plot was then determined by random number (Greig-Smith 1983). Plots were duplicated on larger surfaces, T4, T5, to assess between plot variability. All vascular species inside each plot were recorded and any additional species outside the plot noted. Five 1m x 1m quadrants were positioned by random number co-ordinates within the plot (Greig-Smith 1983) and each species scored for cover-abundance using the 10 point Domin scale (Westhov and Van der Maarel 1973, Kershaw 1985) (Table 1.8).

Table 1.8 Domin Scores and Transformed Computational Values

+	isolated,	cover small	0.04
1	very scarce,	cover small	0.2
2	scarce,	cover small	0.4
3	scattered,	cover small	0.9
4	abundant,	cover c. 5%	2.6
5	abundant,	cover c. 20%	3.0
6	cover	25 - 33%	3.9
7	cover	33 - 50%	4.6
8	cover	50 - 75%	5.9
9	cover	75 - 95%	7.4
10	cover	95 - 100%	8.4

Cover-abundance values were transformed to correct for non-linearity with respect to cover and frequency, (Table 1.8; Bannister 1966), and classified by cluster analysis (Whittaker 1978, Everitt 1980, Gordon 1981). Normalised Euclidian distance (Sokal and Sneath 1973, Orloci 1978) with complete linkage (Fisher and Van Ness 1971,

Johnson 1974, Hartigan 1975, Milligan 1980) was the procedure chosen and run using an IBM personal computer statistics package, SYSTAT. (Wilkinson 1986).

1.5.2.2 Results and Discussion

(a) Species Area Relationship

The number of species on T4 did not differ significantly between the three areas investigated ($p < 0.45$) nor did the site by quadrat size interaction ($p < 0.45$). This suggests it is quite reasonable to infer that the three samples were drawn from the same population, even though species distributions will almost certainly violate the assumptions required for strictly valid Analysis of Variance (Greig-Smith 1983). Therefore, data were merged to give a mean species-area curve for the fourth terrace (Fig. 1.22). This clearly shows 10m x 10m plots were sufficient to adequately sample short tussock grassland flora.

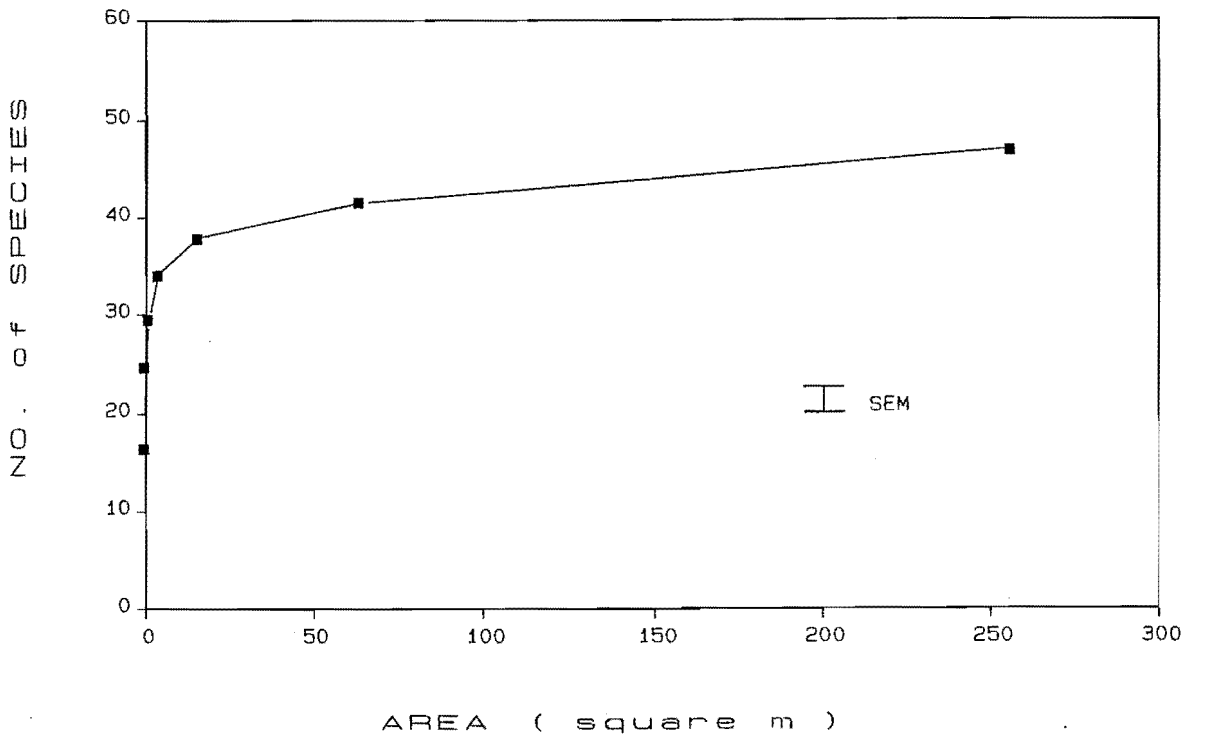


Figure 1.22 Species-area curve in fescue tussock grassland, T4.

Table 1.9 Species Cover-abundance Scores on Terraces T1 - T5.

SPECIES	PLOT 1	2	3	4a	4b	5a	5b	TOT
Festuca novae-zelandiae	2.24	3.50	3.20	2.92	2.34	3.10	2.86	**20.16**
Anthoxanthum odoratum *	3.74	2.76	2.60	2.76	1.24	1.82	2.76	**17.70**
Discaria toumatou	3.94	2.58	2.84	1.66	.72	2.38	3.17	**17.29**
Poa colensoi		2.60	2.42	2.92	3.02	2.24	1.90	**15.10**
Agrostis tenuis	3.06	.72	.40	.26	.80	2.08	3.68	**11.00**
Coprosma petrei		2.08	1.38	1.00	1.72	1.40	.02	**7.60**
Hypochaeris radicata *	.23	1.14	1.92	.90	.90	.50	.42	**6.01**
Hypnum cupressiforme		.95	1.48		.65	.62	1.66	**5.36**
Raoulia subsericea		.18	1.04	.90	2.26	.34	.18	**4.90**
Celmisia gracilenta		.56	1.38	.70	.70	.28	.04	**3.66**
Leucopogon fraserii	.28	.40	.60	.36	.40	.21	.16	**2.41**
Gentiana serotina		.01		.72	.90	.32	.12	**2.07**
Wahlenbergia albomarginata	.08	.70	.40	.36	.40	.13		**2.07**
Pimelea oreophila		.62	.28	.29	.60	.13	.02	**1.94**
Luzula rufa		.60	.56	.14	.25	.12	.12	**1.79**
Anisotome aromatica		.32	.14	.24	.33	.04		**1.07**
Polytrichum juniperinum		.20	.32	.02	.17		.01	**0.72**
Senecio bellidiodies		.21	.01	.14	.14	.12	.08	**0.70**
Rumex acetosella *		.04	.36	.02	.24		.02	**0.68**
Carex breviculmis	.01	.24	.01	.02	.36			**0.64**
Linum catharticum *	.01	.02		.21	.36		.01	**0.61**
Deyeuxia avenoides		.18		.08	.29	.01		**0.56**
Racomitrium lanuginosnum			.01	.18	.13	.18	.01	**0.51**
Hieracium pilosella *	.01	.04	.08	.04		.26		**0.43**
Acaena caesiiglauca			.26			.08	.06	**0.40**
Elymus scabrum	.11	.15		.02	.01	.01	.09	**0.39**
Rytidosperma gracilis	.38						.01	**0.39**
Crepis capillaris *	.08	.12				.10	.05	**0.35**
Scleranthus uniflorus				.18	.12	.04	.01	**0.35**
Viola cunninghamii		.24			.06		.04	**0.34**
Cerastium fontanum *	.13	.08	.04	.02	.06			**0.33**
Helichrysum filicaule						.25	.08	**0.33**
Geranium sessiliflorum		.20	.01	.02	.09			**0.32**
Trifolium repens *				.22	.09			**0.31**
Gonocarpus aggregatus			.08	.05	.04	.04		**0.21**
Coprosma atropurpurea			.01				.18	**0.19**
Aciphylla aurea		.15			.01			**0.16**
Anisotome filifolia		.09						**0.09**
Ophioglossum coriacea			.01	.01				**0.02**
Microseris scapigera							.02	**0.02**
Rock		1.04	.58	1.58	1.14	.38	.01	**4.73**
Bare Ground			3.02	1.07	.44			**4.53**
Litter	1.20	.40	.40	.32	.20	.34	.16	**3.02**

where * indicates a naturalised species and blank = not recorded.

(b) Floristic Analysis

Grassland composition differed between the Craigieburn and Puffers Stream sites (Chapter 7.3). Cover-abundance scores for the major species are shown for each terrace in Table 1.9. Species with very low (0.01) cover-abundance scores not included in Table 1.9 were: *Celmisia spectabilis and Holcus lanatus* on T2; *Craspedia uniflora and Epilobium glabellum* on T3; *Muehlenbeckia axillaris* on T4a and *Cardamine debilis, Lachnagrostis filiformis* and *Microtis oligantha* on T5b. All species occurring in the Puffers Stream site, as delineated in Fig. 1.3, are listed in Appendix 1.3.

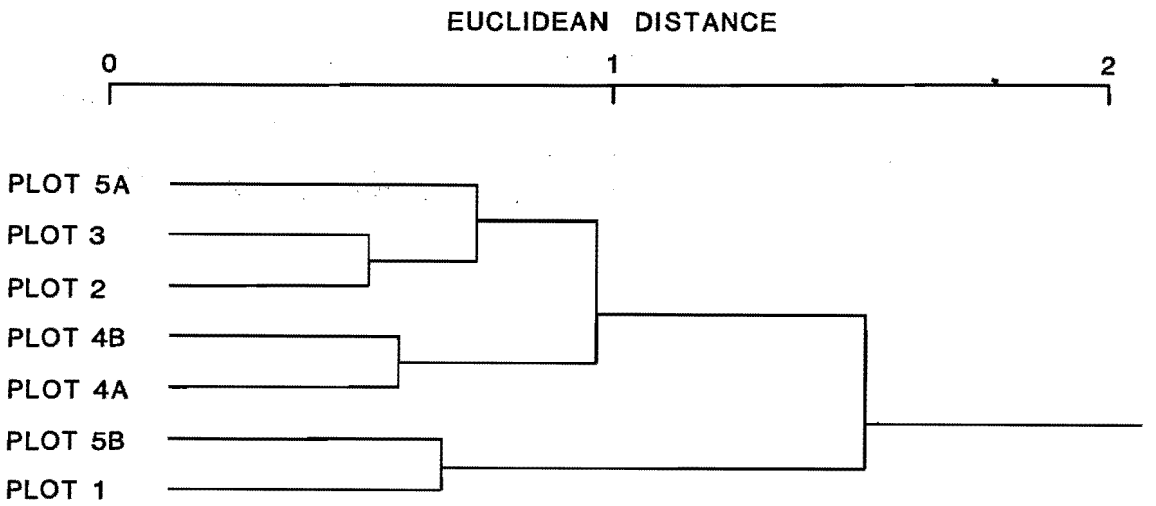


Figure 1.23 Classification dendrogram of the Puffers Stream vegetation T1-T5

The classification dendrogram shows the floristic relationship between terrace vegetation (Fig. 1.23). There are two groups: (a) scrub / grassland (*Discaria > Anthoxanthum > Festuca*; Plots 1, 5b) and (b) grassland with scrub (*Festuca > Agrostis > Discaria*; all other plots). Further division in the grassland plots may reflect subtle differences but cannot be pressed due to the limited sample size. Nevertheless, it is interesting to note that, with the exception of plot 5b, groups exactly match differences in soil parent material: alluvium, debris flow deposits, loessial alluvium and morainic deposits.

The separation of the terrace five plots and the unity of the terrace four plots is almost certainly due to differences in soil variability on each terrace. Soils are uniform on terrace four while profiles on terrace five vary from free draining (Plot 5a) through

to those with impeded drainage and perched gley horizon (Plot 5b, Section 1.4.3). Fertility may also vary, being locally higher adjacent to outcropping rock (Section 1.4.4) The retention and availability of water together with fertility explain differences between plots and the similarity between plot 5b and terrace one. Edaphic relationships are examined more fully in Chapters 2, 3 and 4.

The Puffers Stream grasslands are floristically very similar to others described in the Waimakariri and elsewhere in the montane eastern South Island. Releves near Broken River, Mt Gog and Cloudy Hill, show an almost identical species composition, differing only in minor species Connor and Macrae (1969). The main difference was the lower abundance of *Anthoxanthum odoratum* relative to Puffers Stream. Composition of other Waimakariri valley grasslands is also very similar (Malcolm 1925, Sewell 1947, Moffat 1956, Burrows 1977), though there is an increased frequency towards Cass of such species as *Cassinia fulvida, Cotula squalida, Blechnum penna-marina* and *Lycopodium fastigiatum*, possibly due to greater precipitation. The Puffers Stream grasslands are very similar to Connor's (1965) phase C Fescue tussock grasslands on morainic downs and outwash in the adjacent Rakaia catchment and his phase F mature fescue tussock grasslands, on similar terrain, in the Mackenzie (Connor 1964). Here, *Festuca novae-zelandiae, Poa colensoi, Coprosma petrei, Discaria toumatou* and *Raoulia subsericea* were the most important native species. Connor's data shows the adventive grasses *Anthoxanthum odoratum* and *Agrostis tenuis*, in the Mackenzie and Waimakariri, to be less abundant compared with the Puffers Stream data. However this only reflects incomplete colonisation when Connor surveyed: both species have since strikingly expanded in the Mackenzie (Espie *et al.* 1984), giving grassland phases now almost identical to those at Puffers Stream.

It is impossible to reconstruct the antecedent grassland with certainty from the existing flora. Red tussock occurs in riparian areas in the study site and on morainic deposits nearby. Originally red tussock grasslands may have extended on to the outwash surfaces. However, no species distinctly associated with red tussock (Connor 1964) occurred excepting the debatable *Anisotome aromatica.* Conversely, species characteristic of Tall tussock grassland eg. *Celmisia spectabilis, Aciphylla aurea* and *Cyathodes colensoi* are present. Whether they are relicts from a previous tall tussock grassland or are mere opportunists from adjacent grassland 200m - 300m higher in elevation is unclear. Most probably there was a tall tussock grassland with *C. rubra* as the major species but with *C. macra* and *C. flavescens* also occurring.

Quantitative botanical data from early studies in the Waimakariri were re-analysed statistically using analysis of variance. There was no significant difference ($p < 0.56$) in species composition or cover between grazed Cass grasslands or those spelled from grazing between 1917 - 1925 (Malcolm 1925). Nor did the density of fescue tussock differ significantly with grazing ($p < 0.156$). Ungrazed densities were 11.8 vs 15.2 tussocks m^{-2} when grazed. Effects of grazing at four sites were later investigated in 1946 by Sewell (1947). His sites were:-

Bailey,	toeslope,	near Grasmere,	S66:21 (7-9) 13 (5-7)
Long hill,	valley tce,	Slovens Creek,	S66:27 (2-3) 11 (8-9).

Craigieburn,	toeslope,	Slovens Creek,	S66:32 (9) 089 -091.
Marymere,	hillslope,	Slovens Creek,	S66:23 (2-4) 07 (3-5).

One year's exclosure did not significantly alter species composition or cover. Nor was there any significant site by grazing interaction. Sites did, however, differ significantly in species cover, although Sewell did not mention this.

It is impossible to use Sewell's data for precise species comparison as unfortunately he lumped together into one category all attached dead matter and litter, irrespective of species. Probably most of his dead material was attached dead *Festuca novae-zelandiae* leaves, but attempts to partition it using his live: dead leaf ratio data gave anomalous results. Nevertheless, the broad similarity with the Puffers Stream sites is apparent. Interestingly, *Agrostis tenuis* is not specifically mentioned. Evidently, it was still expanding its range.

Ten years later, the three Slovens Stream sites were re-examined using the same methodology (Moffat 1956). Analysis of variance comparing the two sets of data showed a highly significant increase in cover (33.6% - 67.8%; $p < 0.001$). Sites differed ($p < 0.01$) as did species ($p < 0.001$). Although differences due to grazing were not significant, individual species responded to grazing differently as indicated by a highly significant interaction ($p < 0.001$). *Festuca novae-zelandiae*, and 'Dead' increased in ungrazed plots while *Hypochaeris radicata* and *Anthoxanthum* decreased (Fig. 1.24).

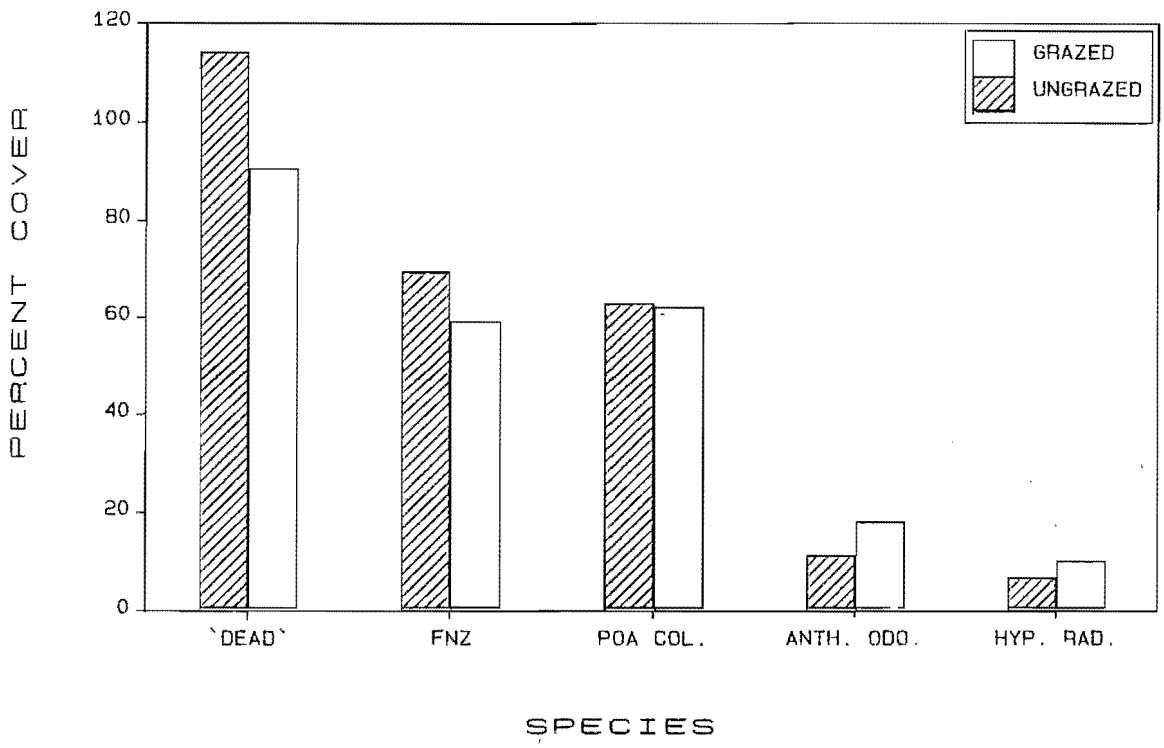


Figure 1.24 Change in species cover after 10 years removal from grazing.

Furthermore,the proportion of species cover changed, i.e. the year by species interaction was highly significant ($p < 0.001$). This was primarily due to the massive increase in 'Dead matter' and *Poa* in 1956, but also to the decrease in *Anthoxanthum* (Fig. 1.25).

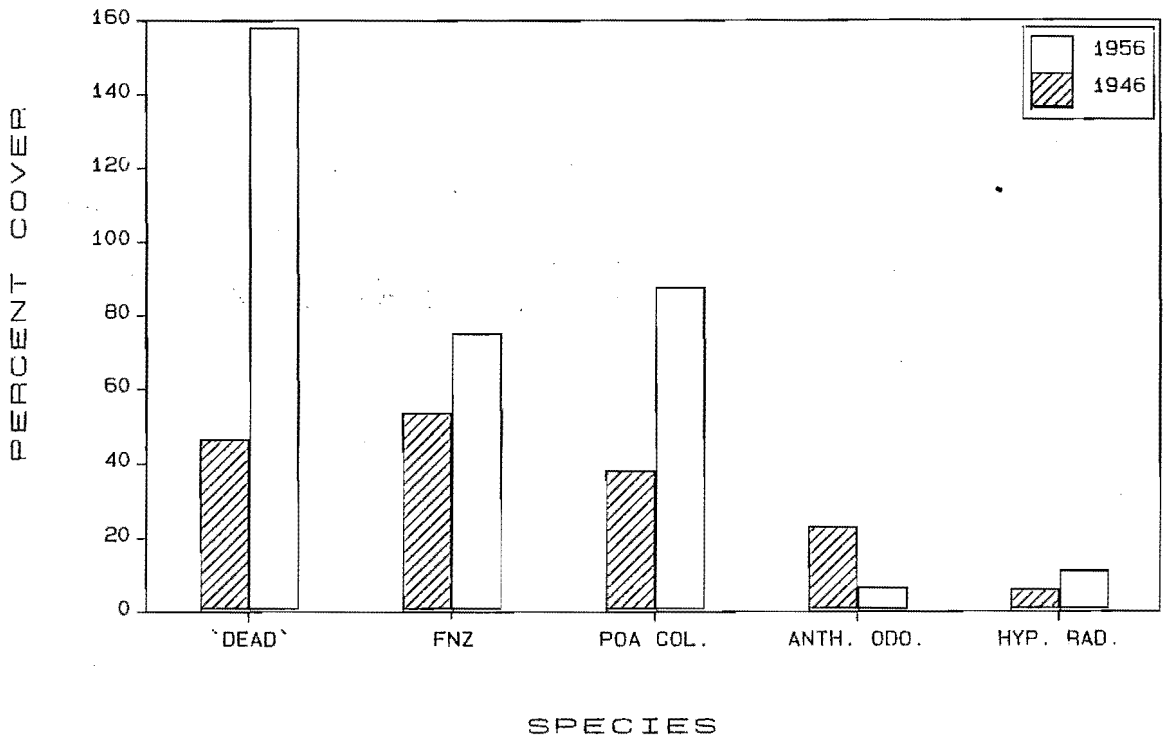


Figure 1.25 Change in species cover Waimakariri fescue grasslands 1946 - 1956.

In summary, these studies suggest that the floristic response to removal of grazing is slow. Species behaviour was not consistent between studies nor between sites in the same study. Limited replication makes it impossible to generalise many metres beyond the sample plots. Furthermore, how rigorously Moffat followed Sewell's methodology, in particular his actual judgment in scoring pin hits, is not clear. Part of the difference ascribed to change may be due to methodology. However, what is clear is that the floristic composition of the valley grasslands in the Waimakariri has remained substantially unchanged during the last fifty years. The major exception is the relatively

recent expansion of exotic grasses. Currently, the ingress of *Pilosella (=Hieracium)* species, as described by Rose (1983) in the adjacent Harper - Avoca catchment has not progressed, as yet, very far.

Plate 2.1 Fescue tussock *Festuca novae-zelandiae*

SECTION 2 : FESCUE TUSSOCK GRASSLAND ECOLOGY

CHAPTER 2: DISTRIBUTION OF FESTUCA NOVAE-ZELANDIAE AND DISCARIA TOUMATOU ON A SEQUENCE OF HIGH COUNTRY YELLOW BROWN EARTH SOILS

2.1 INTRODUCTION

Fescue or hard tussock, *Festuca novae-zelandiae* (Hack.) Cockayne, is a perennial grass dominating the physiognomy of montane short tussock grassland throughout New Zealand (Cockayne 1928). Short tussock grassland comprises 8.1% of New Zealand's surface cover, 24,300 ha in the North Island and 2,146,000 ha in the South (Fig. 2.1; Hunter and Blaschke 1986). Fescue tussock is the most widespread tussock in short tussock grassland, occurring throughout the hill and high country of the eastern South Island and the volcanic plateau in the North. Short tussock associations are listed in Appendix 2.1 .

Matagouri, or Wild Irishman, *Discaria toumatou* (Raoul) is an indigenous shrub often co-dominant with fescue tussock in eastern South Island intermontane basins and valleys (Appendix 2.1). Its distribution has been recorded and mapped by Bascand and Jowett (1981) and Hunter (1986). Fifty-five percent of the soils where matagouri was recorded were classified as brown-grey or yellow-grey earths (Hunter 1986). On more strongly developed soils the extent of matagouri is reduced and it is often strikingly confined to rejuvenated surfaces, fans, debris flows and recent alluvial soils (Cutler 1977). Matagouri is nodulated and capable of symbiotic N fixation up to 67 kg N ha year (Morrison and Harris 1958, 1959, Morrison 1961, Scott 1968, Daly 1969). The biology of matagouri has been comprehensively reviewed by Daly (1967, 1969) and Scott (1986).

The floristic composition of fescue tussock grasslands has been extensively described (Cockayne 1916, Cockayne and Foweraker 1916, Oldridge 1922, Malcolm 1925, Cockayne 1928, Sewell 1947, Wilton 1948, Barker 1953, Moffat 1957, Thornton 1958, Scott, 1959, Calder 1961, Connor 1964, 1965, Connor and MacRae 1969, Moore 1976, Burrows, 1977, Makepeace 1980, Rose 1983, Espie *et al.* 1984) however comparativly little is known about the autoecology of the tussock or matagouri. The predominant emphasis of short tussock grassland studies has been agronomic improvement (Scott 1977, O'Connor 1986).

Fescue tussock research is briefly summarised below to provide the general context for this and following chapters. Connor and Cook (1955), investigating the tussock's breeding system, demonstrated that *F. novae-zelandiae* was an outcrossing species. Connor (1960), after examination of leaf morphology from extensive collections of garden grown tussocks, found significant differences between *F. novae-zelandiae* and *F. mathewsii* but anatomical variability precluded the use of leaf morphology as a taxonomic criterion. Connor (1963) also described the development pattern of flowering stem growth at two Canterbury sites. Scott (1959, 1960) examined climatic influence on phenology. Flowering was later at higher altitudes and on shaded aspects. He also briefly measured daily growth rate under controlled conditions (Scott 1961b) and investigated the growth response to temperature (Scott 1961c, 1970). Relative growth rates of fescue tussock were low initially and the optimum temperature for maximum growth differed between low and high altitude forms of fescue tussock.

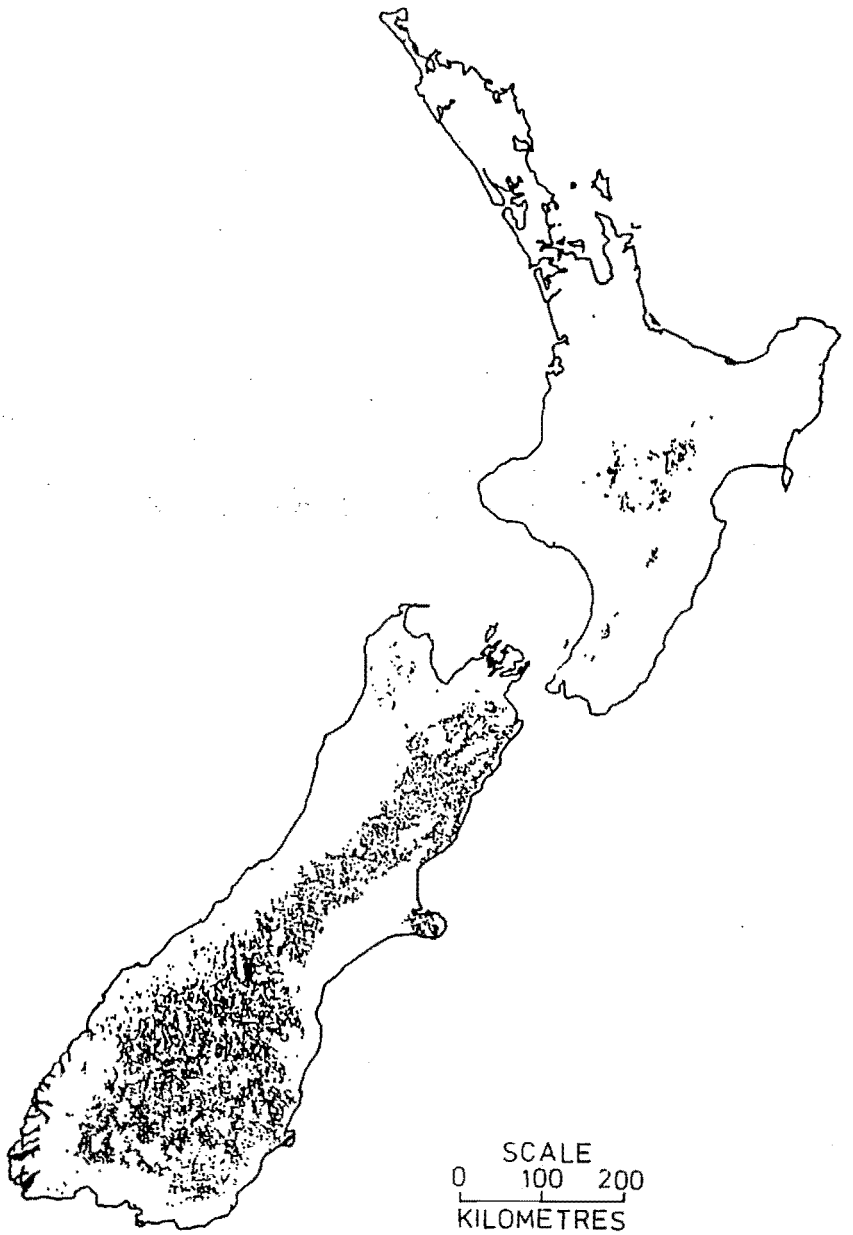


Figure 2.1 : The distribution of short tussock grassland in New Zealand (Hunter and Blaschke 1986)

Scott (1961a) demonstrated inter-tussock species zonation occurring in fescue tussock grassland. Radcliffe (1974), Scott and Archie (1976) and Scott and Wallace (1978) investigated the effect tussocks on the establishment and growth of inter-tussock plants. Dunbar (1970, 1974) and Dunbar *et al.* (1977) examined how fertilisers and cover affected seedling establishment of fescue tussock on eroded mountain subsoils.

Morrison (1958) in a pot trial with a Tekoa soil from Bealey found large responses to nitrogen (N) plus phosphorus (P) but little response to potassium or sulphur (S) without both N and P. Nutrient amendment also altered the distribution of leaf sclerenchyma and tussock digestibility in another pot experiment (O'Connor pers. comm.). In a field trial on Craigieburn soil, O'Connor (1961) obtained a significant herbage response to a combination of N + P + S but responses to the individual nutrients differed little from the control while N application alone even depressed yield. O'Connor (1965) showed lax cutting resulted in greater leaf growth compared with tussock cut short and later (O'Connor 1967a) found N application increased basal areas of uncut tussock but decreased the area of cut tussock. Burning snow tussock (*Chionochloa rigida)* grassland increased fescue tussock yield 4-5 times (O'Connor and Lambrechtsen 1964).

Moore (1976) recorded vegetation changes over 30 years in permanent quadrats at Molesworth Station, Marlborough. Fescue tussock seeding establishment was very low, particularly when rabbits were present, and clonal spread by fragmentation was more important. Longevity of individual tussocks was estimated to exceed 50 years. The phytomass of a degraded fescue tussock community has been comprehensively determined by Evans (1980) in the Craigieburn Range.

The most detailed field study of fescue tussock was Sewell's (1947, 1952) investigation of seasonal and grazing effects on tussock size, growth and cover at four Waimakariri sites. He also briefly assessed the effect of burning. Wilton (1948) and Moffat (1956), using Sewell's plots, found protection from grazing for two or ten years resulted in little change in species composition or cover. With fertiliser application however, O'Connor (1967a) demonstrated an interaction between grazing and fertility : both altered fescue tussock density, morphology and flowering. O'Connor (1986) has recently reviewed the role of grazing in the historical derivation of the fescue tussock grasslands.

The biochemical composition and digestibility of fescue tussock has been investigated by Coop *et al.* (1953), Allen (1975) and M^{c}Kenzie (1978). Dryden and Archie (1980) found fescue tussock so low in feed value that penned sheep, fed only fescue tussock, were on a negative energy balance.

Makepeace *et al.* (1985) recently demonstrated competition with mouse ear hawkweed (*Pilosella officinarum*) decreased stature and leaf N and P concentration. The phenolic, *umbilliferone*, present in mouse ear leaves, reduced fescue root growth, though field allelopathy was not demonstrated. Kelsey (1957) and Harrison and White (1969) recorded the insect species attacking fescue tussock.

From this research summary it is evident that the population structure and variability of fescue tussock has not been comprehensively investigated nor has the influence of edaphic factors . This information is necessary for understanding the biology of fescue tussock and for the future management of fescue tussock grasslands. Therefore this study had two main aims :

1. To determine quantitatively the size and variability in biomass, composition and live shoot nutrient pools in a typical fescue tussock population and establish the relationship between tussock morphology and biomass.

2. To relate the density and aerial growth of fescue tussock and matagouri on an development sequence of soils to soil chemical factors and determine the influence of pedological development.

2.2 MATERIALS AND METHODS

2.2.1 Fescue tussock density and morphology on T1 - T5

The number of individual tussocks and their basal circumference were recorded in 10 x 10 m plots (Kershaw 1967). Plots were located on each of the five sequential terrace surfaces T1 - T5 (Chapter 1) using a 100 m tape, positioned north-south (parallel to Puffers Stream) from a subjectively chosen origin in representative grassland. (the limited area of the lowest terrace, T1, required using only 30 m orientated east-west). Each plot was located on the tape by random number and divided into four 5 x 5 m blocks. Within each block, five 5 x 1 m quadrats (Greig-Smith 1985) were pegged and marked with tape. Plots were duplicated on the two largest surfaces, T4 and T5, to assess variability between plots.

Tussocks density and basal circumference were recorded in each quadrat using the following criteria. An individual tussock was defined as a "visually discrete group of tillers which appeared to grow from one origin". Fescue tussocks are usually easy to define (Laycock and Batcheler 1975), but there were two situations where definition of an individual was problematic : (a) when two tussocks grew in close proximity with intersecting basal circumferences and (b) when the central tillers of senescent tussocks had decomposed leaving an often incomplete circumference of peripheral tillers. The former was very difficult to distinguish from an irregular elliptical individual and the latter from several small tussocks which naturally occurred in a semi-circular configuration.

The following criteria were used to define the entity to be recorded.

1. An elongated elliptical group of tillers was deemed two individual tussocks unless an external factor, e.g. proximity to shrub or rock, could have influenced the growth pattern, as Scott (1961b) found tussock circumferences tend to be semi-circular. Such groups were arbitrarily split at the mid-point of the major basal axis and each fraction measured as an individual.

2. Quasi semi-circular configurations of small tillers were regarded as individual small tussocks unless dead matter or circular linkage, partial or complete, of two-thirds of the tillers indicated a remnant senescent tussock.

3. Tiller groups falling on plot boundaries were included if more than 50% of their basal area fell inside the plot. Tussocks exactly divided were included on north and south plot margins but excluded on the east and west.

Basal circumference was classed in three categories using a tape drawn "fairly tightly" (Williams 1977) round the base of each tussock 1 cm above ground level:-

(a)	Small	< 6.5 cm	circumference
(b)	Medium	> 6.5 to < 30 cm	circumference
(c)	Large	> 30 cm	circumference

Ten additional 1 x 1 m quadrants were used to measure exact basal circumferences. Two random numbers set the distance along the sides of the plot and positioned the quadrat. The basal circumference of every tussock was measured with a tape ± 5 mm. The height of each tussock was measured vertically from ground level to the uppermost leaf extended on a 1 mm graduated ruler to ± 5 mm (Mark 1965; Williams 1977). The longest flowering stem, when present, was similarly measured to the uppermost part of the inflorescence (Mark 1965).

Fescue density, morphology and biomass were correlated with 30 soil chemical parameters, sampled by 10 cm depth increments, for terraces T1 to T5 (Harrison and Swift 1984). The soil variables and their coding are given in Appendix 2.2.

2.2.2 Matagouri density and morphology on T1 - T5

Individual matagouri shrubs, an individual being loosely defined as "a visually discrete plant which appeared to grow from one origin" were counted in each 5 x 5 m block per plot (Section 2.2.1). This definition, although imprecise, avoids the problem of identification of an individual, which can be difficult as different genets can intertwine below ground level giving the appearance of a single plant.

The maximum natural height, maximum breadth, and maximum length, perpendicular to breadth of each individual was measured by ruler to ± 1 cm. A crude estimate of aerial volume was calculated by multiplication of these values

2.2.3 Variability in fescue tussock morphology and mineral content on T4

To establish the variability occurring in a natural fescue tussock population, fifty two fescue tussocks were randomly sampled in a 30 x 30 m quadrat on the main surface, T4, immediately due north of the main experimental plot on 9 March 1981 (Fig. 1.6). Tussocks were defined and measured as in section 2.2.1 then carefully removed with an intact 3-5 cm root turf, transported to Lincoln College and immediately stored at -3.0 °C.

The tussocks were remeasured in the laboratory after thawing. The maximum basal circumference was determined with a thin wire pulled to a standard tightness round the tussock base within 1 cm from ground level. After complete fractionation, the longest leaf, either live or dead, was measured from the base of the sheath to the leaf tip extended on a 1mm graduated ruler ± 0.5mm. The longest flowering stem was similarly measured to the most distal part of the inflorescence (Mark 1965).

There was no significant difference between field and laboratory measurement of any fescue tussock morphological parameter. Regression equations were all, as expected, with intercepts close to zero and regression coefficients close to unity (Table 2.1). Field measurement of flowering stem height was the most accurate with precision decreasing slightly for basal circumference and leaf length.

Table 2.1: Linear regression equations for laboratory and field measurement of fescue tussock morphology; where LTH = extended leaf length, BC = basal circumference, FC = flowering stem length and ( ) = std. error of the parameter.

Lab LTH	=	-1.080 (1.535)	+ 1.028 (0.045)	Field LTH	r = .933
Lab BC	=	-0.147 (0.532)	+ 0.929 (0.032)	Field BA	r = .957
Lab FC	=	-0.030 (0.460)	+ 0.989 (0.010)	Field FC	r = .996

There was no significant difference between two observers measuring fescue tussock basal circumference in the field. Twenty-one tussocks in three plots were independently measured with the following results :

Observer A	=	0.019 (0.482)	+ 1.018 (0.025)	Observer B	r = .968

where ( ) = std. error of the parameter.

In the laboratory tussocks were fractionated into four classes :

1. Live Shoot : Lamina and sheath where more than 10% of the lamina tissue was green. Distal dead tip tissue (Williams 1977) was not removed unless it exceeded 20% of the lamina.

2. Recent Dead Shoot : Lamina, sheath, removed lamina tip and flowering culm, either yellow or light straw coloured, or where less than 10% of the lamina tissue was green.

3. Old Dead Shoot : Lamina, sheath and flowering culm bleached light to dark grey.

4. Live Flowering Shoot : Lamina, sheath, culm and inflorescence where more than 10% of the flowering culm was green.

Fractions were dried in a forced draught oven at 70 °C for 48 hrs and weighed ± 0.05 g. Live fractions were bulked for each tussock, ground for 30 seconds in a Tema mill to pass a 1.0mm mesh sieve and stored for chemical analysis.

Nitrogen was determined using a micro-kjeldahl method (Allen 1974), phosphorus and sulphur by nitric-perchloric acid digestion and autoanalysis (Appendix 2.3).

2.2.4 Estimation of fescue tussock aerial biomass from morphological parameters

To determine the relationship between non destructive measurements of tussock morphology and above ground biomass 400 tussocks were measured, as specified in section 2.2.1, on T4 immediately due north of the main experimental plot. Tussocks were carefully harvested, taken to Lincoln College and immediately oven dried at 70 °C for 48 hrs and weighed ± 0.05 g. In addition one of the largest tussocks in the study area was harvested from T2 to indicate values obtained near the apparent upper limit of fescue tussock size.

Basal area was more closely related than leaf length to total tussock aerial biomass. The relationship was curvilinear for both parameters and therefore square root and $\log_e$ transformations improved the linear fit (Table 2.2). All combinations of transformations were tested with the best single factor regression, $\log_e$ basal area accounted for over 90 % of the variance in $\log_e$ DM (Fig. 2.2).

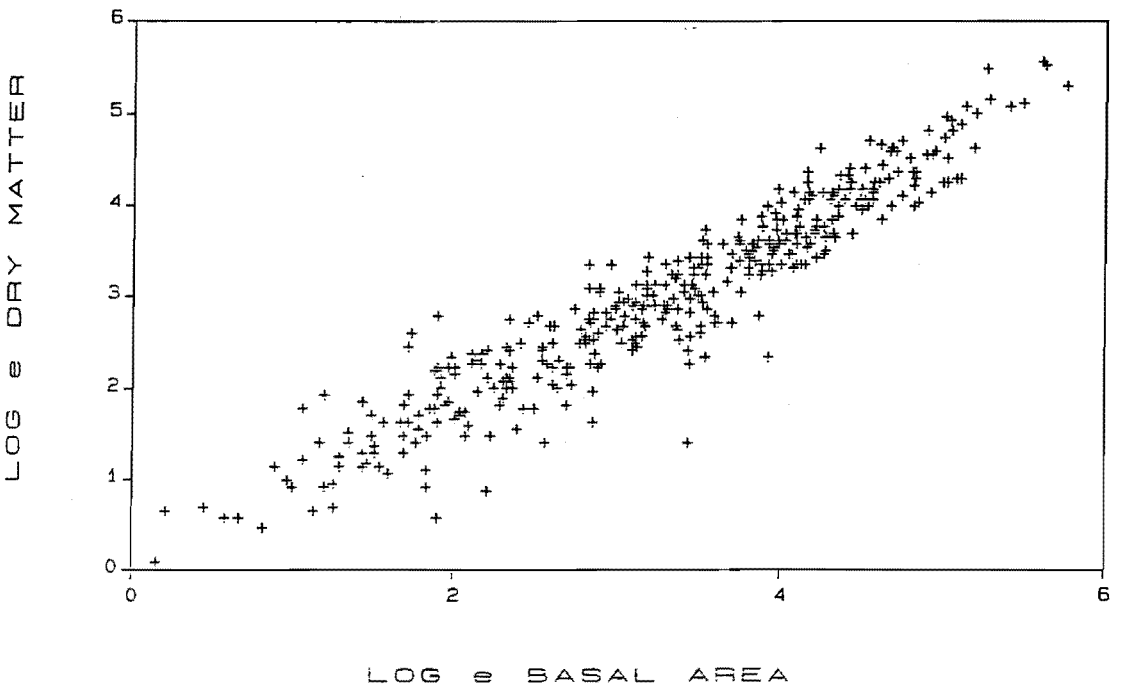


Figure 2.2 : The relationship between fescue tussock $\log_e$ basal area and $\log_e$ shoot DM (n=400).

Table 2.2 : Linear Regression equations for fescue tussock morphology and aerial biomass where DM = total dry matter, BA = basal area, LTH = extended leaf length and ( ) = standard deviation of the parameter.

DM	=	-3.58 (1.34) + 0.813 BA (0.020)	$r = 0.895$	***
$\sqrt{DM}$	=	2.58 (0.05) + 0.054 BA (0.001)	$r = 0.933$	***
$\log_e DM$	=	0.054 (0.050) + 0.888 $\log_e$ BA (0.015)	$r = 0.949$	***
DM	=	-97.6 (6.18) + 4.03 LTH (0.185)	$r = 0.737$	***
$\sqrt{DM}$	=	-4.20 (0.330) + 0.283 LTH (0.010)	$r = 0.820$	***
$\log_e DM$	=	9.36 (0.489) + 3.56 $\log_e$ LTH (0.142)	$r = 0.783$	***

Stepwise linear regression gave excellent empirical predictive equations (Table 2.3). All combinations of natural and transformed parameters (ie DM, $\sqrt{DM}$, $\log_e$ DM and DM^2) for each variable were tested. Log and square root transformed DM models were slightly better than natural DM but all models showed no improvement by fitting more than two terms. The three equations with the highest correlation coefficients are shown in Table 2.3.

Table 2.3 : Multiple Linear Regression equations for fescue tussock morphology and aerial biomass where DM = total dry matter, BA = basal area, LTH = extended leaf length and ( ) = standard error.

DM	=	-11.6 28 (1.696) + 0.002 BA^2 (0.000)	+ 0.030 LTH^2 (0.002)	$r = .949$	***
$\sqrt{DM}$	=	-0.359 (0.078) + 0.628 $\sqrt{BA}$ (0.016)	+ 0.0015 LTH^2 (0.0001)	$r = .969$	***
$\log_e DM$	=	-1.767 (0.127) + 0.724 $\log_e BA$ (0.016)	+ 0.416 $\sqrt{LTH}$ (0.027)	$r = .968$	***

2.2.5 Statistical Analysis

Analysis of variance, in the general statistics package GENSTAT (Alvey *et al.* 1982), was used to test the significance of treatment effects. The validity of the assumptions required for ANOVA in GENSTAT were checked by (a) plotting residuals against fitted values and (b) by CSIRO macro sub routines appended in GENSTAT.

Regression and correlation analyses were run using the statistics package SAS (SAS Institute 1985).

Significance levels throughout the text are indicated as follows : *** $p \leq 0.001$; ** $p \leq 0.01$; * $p \leq 0.05$; ns $p > 0.05$. SEM = the Standard Error of a Mean. The pooled SEM for treatment or interaction terms has been used to indicate variability when data has been presented in figures (Alvey *et al.* 1982).

2.3 RESULTS

2.3.1 Fescue tussock density and morphology on T1 - T5

Tussock density differed between terraces ($p < .001$) with density on T2 being nearly twice the density of all other terraces (Table 2.4). Density was lowest on T1 and T5 plot a. Density estimates on T1-T5 from 1 m^2 quadrats did not differ significantly from estimates from 5 x 5 m quadrats (mean 6.3 vs 5.5 tussocks m^{-2}; $p < .115$). The standard errors show, as expected, more variability with the small quadrats. Variability between 1 x 1 m plots was small on T4 and large on T5 (Table 2.4), consistent with soil variability (Chapter 1.5).

Table 2.4 : Fescue tussock density T1-T5 recorded in different quadrat sizes (No. Live tussocks m^2 ± SEM).

Terrace and Plot	1 m^2 quadrat	25 m^2 Plot
T1	4.0 ± 0.6	3.2 ± 0.3
T2	13.6 ± 2.8	11.0 ± 0.5
T3	5.2 ± 0.7	5.7 ± 0.3
T4a	5.2 ± 0.8	5.0 ± 0.3
T4b	5.9 ± 0.4	4.9 ± 0.3
T5a	4.1 ± 0.7	3.2 ± 0.3
T5b	7.4 ± 1.1	no data

Mean tussock basal area (cm^2 $tussock^{-1}$), leaf length and flowering culm length differed significantly between terraces ($p < .001$; Table 2.5). Basal area was lowest on T2 and T5b and highest on T1 and T5a. Leaf length was greatest on T5a and slightly lower on T4 compared with other terraces. Flowering culm length was highest on T2 and T5a.

Table 2.5: Mean tussock basal area, leaf length and flowering culm length T1-T5 (± SEM).

Terrace & Plot	Basal Area (cm^2/tussock)	Leaf Length (cm)	Flowering Culm Length (cm)
T1	48.1 ± 15.1	34.6 ± 3.1	47.6 ± 3.9
T2	18.1 ± 2.9	32.0 ± 1.4	53.4 ± 2.3
T3	43.3 ± 8.9	32.7 ± 1.6	43.1 ± 2.3
T4a	41.7 ± 7.1	26.1 ± 1.1	45.0 ± 1.6
T4b	41.4 ± 7.4	27.6 ± 1.0	42.8 ± 1.8
T5a	54.8 ± 12.8	38.5 ± 2.0	42.2 ± 2.7
T5b	22.0 ± 4.1	29.7 ± 1.2	36.9 ± 1.9

Above ground biomass tussock^{-1} was estimated for each terrace from mean basal area per tussock using the √DM regression equation, arbitrarily chosen over the $\log_e$ DM equation on r value (Table 2.3). Total aerial biomass^{-2} was calculated from these values using the density estimates from 5 x 5 m plots (Table 2.4). Total biomass was greater on T2 and T3 but considerably less on T1, T4 and T5 (Fig. 2.3).

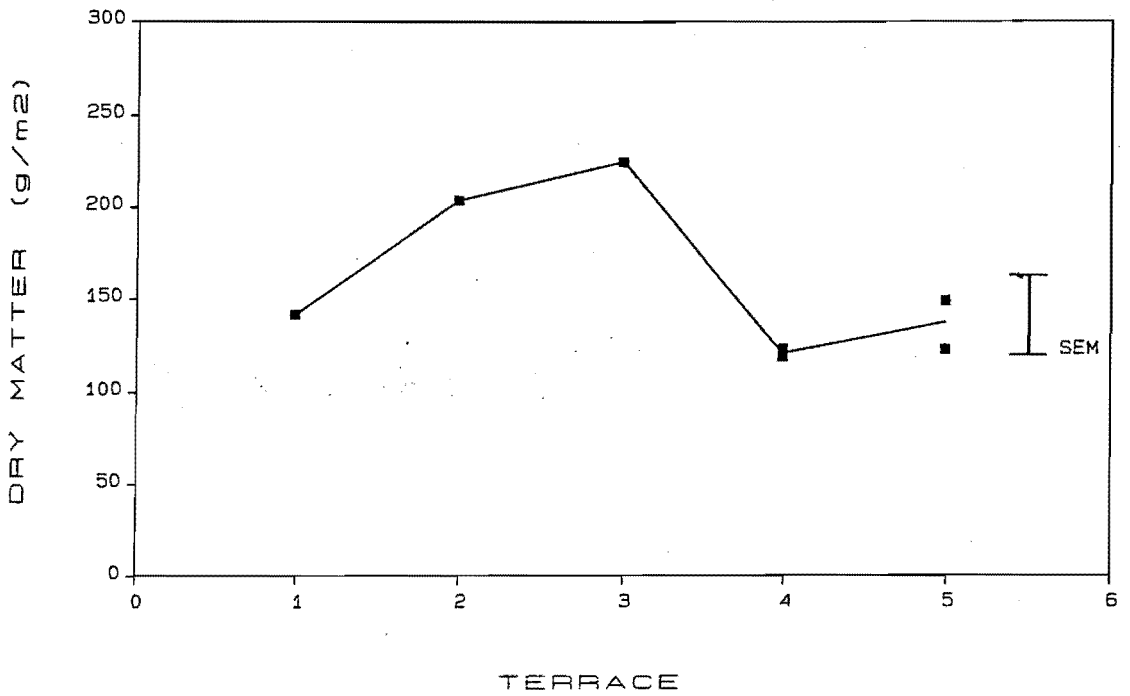


Figure 2.3 : Fescue tussock shoot DM on terraces T1-T5.

2.3.2 The relationship between soil and fescue tussock density and morphology

Correlation analysis was used to investigate the relationship between 30 soil chemical parameters (Appendix 2.2), measured to 100cm depth, and fescue tussock density or basal area tussock^{-1}. All the significantly correlated soil parameters are summarised by horizon depth in Tables 2.5 and 2.6 with the full set of correlations for density listed in Appendix 2.4 and for basal area in Appendix 2.5. In the summary tables if no correlation coefficients were significant then only the most highly correlated variable(s) were presented. Auto-correlation between soil variables has been ignored in these tables as there was no logical criterion for determining which of the variables to omit.

Tussock density was positively correlated with soil total (Ptot, Pxrf) and organic (Porg) P fractions, particularly in the upper profile (0-40 cm). Nitrogen was highly correlated at 10-20 cm depth and cation exchange capacity (CEC) in the subsoil (Table 2.6).

Table 2.6: Correlation coefficients between fescue tussock density and soil chemical variables on T1-T5 ; ( ) = significance level.

Horizon Depth (cm)	Porg	Ptot	Pxrf	Pap	Fe_p	C	N	CEC	AL
0-10	.92 (.03)	.91 (.04)	.87 (.06)	.82 (.09)	.85 (.07)				
10-20	.94 (.02)	.89 (.04)	.89 (.04)			.88 (.05)	.84 (.02)		
20-30	.94 (.01)	.87 (.05)	.88 (.04)			.88 (.05)		.90 (.02)	
30-40	.92 (.03)	.86 (.06)	.85 (.07)		.83 (.08)		.80 (.10)	.87 (.05)	
40-50	.97 (.01)				.96 (.04)		.93 (.07)	.98 (.01)	.95 (.05)
50-60	.85 (.07)	.82 (.09)							
60-70				.74 (.06)					

Mean basal area $tussock^{-1}$ was significantly correlated with topsoil P fractions (Pa, Porg, Ptot), carbon (C) and CEC (Table 2.7). Loss on ignition (LOI, highly auto-correlated with C and CEC), EDTA- and oxalate- extractable aluminium (AL_o) were the most highly correlated variables deeper in the profile. The only parameter showing significant correlation below 50 cm was oxalate extractable iron at 50-60 cm ($r = 0.91$, $p < .03$), but this has not been tabulated.

Table 2.7: Correlation coefficients between fescue tussock basal area and soil chemical variables T1-T5 ; ( ) = significance level.

	Pap	CEC	C	Ptot	Porg	Al_e	LOI	Al_o	Fe_p	H	N
0-10	.95 (.01)	.94 (.01)	.91 (.03)	.87 (.05)	.83 (.08)	.81 (.09)					
10-20		.90 (.04)	.84 (.08)	.78 (.12)	.78 (.12)	.81 (.09)	.85 (.07)				
20-30		.80 (.10)	.80 (.11)			.96 (.01)	.93 (.02)	.78 (.11)			
30-40		.92 (.03)						.99 (.01)	.92 (.03)	.91 (.03)	
40-50						.95 (.06)	.87 (.05)				.93 (.07)

2.3.3 Matagouri density and morphology on T1 - T5

Matagouri density was highest on T2, similar to fescue density, but unlike fescue was much lower on T4 ($p < .001$; Table 2.8). Shrub stature, shown by aerial volume, was far greater on T1 than any other terrace ($p < .001$; Table 2.8). Aerial volume m^{-2} was progressively lower on T2 to T4 but increased on T5 (Fig. 2.4).

Table 2.8: Matagouri density and aerial volume T1-T5 (± SEM)

Terrace & Plot	Matagouri Density (plants m^{-2})	Matagouri Aerial Volume (m^3 m^{-2})
T1	0.8 ± 0.08	1.59 ± .21
T2	1.6 ± 0.12	0.13 ± .06
T3	1.4 ± 0.06	0.07 ± .01
T4a	0.1 ± 0.04	0.22 ± .08
T4b	0.2 ± 0.08	0.04 ± .01
T5a	0.7 ± 0.10	0.54 ± .06
T5b	0.4 ± 0.12	1.02 ± .17

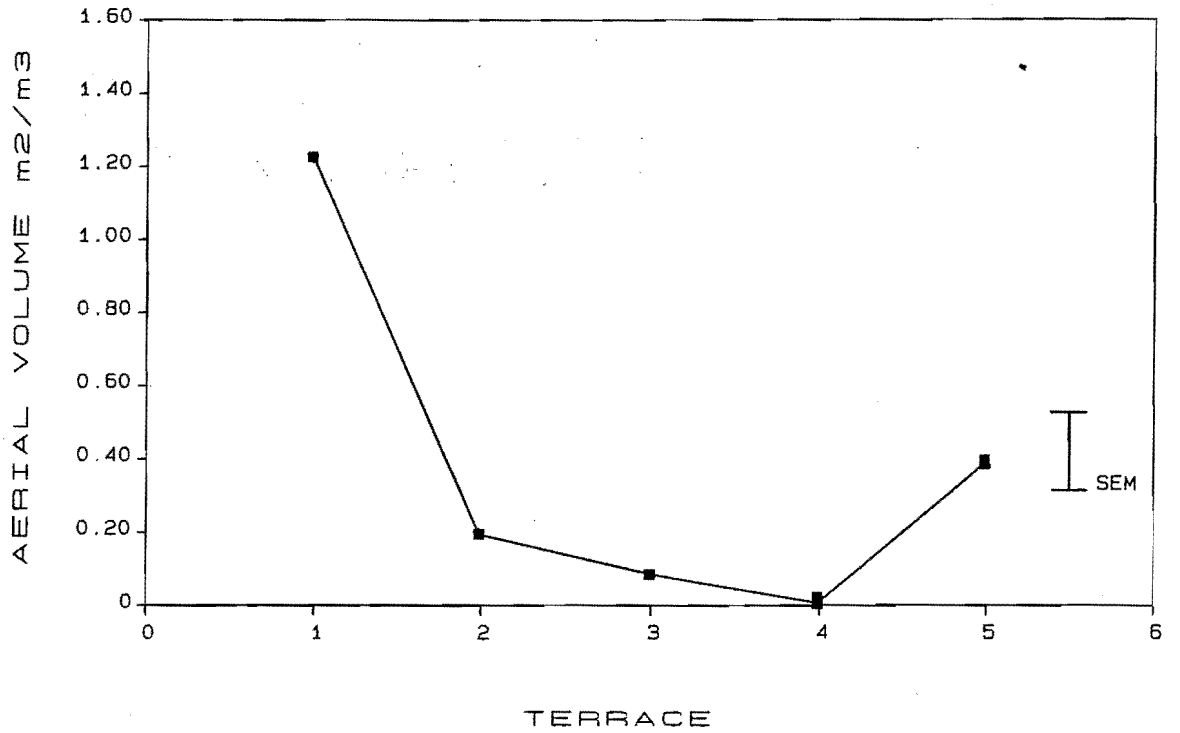


Figure 2.4 : Matagouri shoot aerial volume T1-T5.

Matagouri density and aerial volume was correlated with soil chemical parameters as previously described for fescue tussock. Matagouri density, in sharp contrast to fescue density, showed no significant correlation with any soil parameter above 40 cm depth (Appendix 2.6). P fractions (Porg, Pxrf, Ptot, Pa) below 40 cm depth were the only highly correlated variables in the entire data set and are shown, for all horizons, in Table 2.9.

Table 2.9: Correlation coefficients between matagouri density and soil chemical variables T1-T5; ( ) = significance level; significant values emphasised.

Horizon Depth (cm)	Porg	Pxrf	Ptot	Pa
0-10	.54 (.35)	.48 (.41)	.48 (.41)	.27 (.66)
10-20	.69 (.20)	.61 (.27)	.60 (.29)	.24 (.70)
20-30	.79 (.11)	.70 (.19)	.67 (.22)	.12 (.84)
30-40	.85 (.06)	.83 (.07)	.81 (.10)	.41 (.48)
40-50	.73 (.16)	**.91** (.03)	**.90** (.04)	.85 (.06)
50-60	.60 (.29)	**.90** (.04)	**.91** (.05)	**.89** (.05)
60-70	.29 (.64)	**.95** (.01)	**.95** (.01)	**.94** (.02)
70-80		.88 (.06)	.82 (.09)	.82 (.09)
80-90	.60 (.40)	.48 (.68)	.77 (.23)	.56 (.43)

Matagouri aerial volume was negatively correlated with Al_e, Al_o, P retention (Pret), Fe_p, Al_p, CEC and C between 0-50 cm (Table 2.10; Appendix 2.7). The only significant positive correlations were with exchangeable magnesium (Mg; 20-40 cm), base saturation (BS_C; 20-30 cm) and pH (30-100 cm). Other variables highly correlated between 50-100 cm were Fe_o and NaF (Table 2.10).

Table 2.10: Correlation coefficients between matagouri aerial volume and soil chemical variables T1-T5; ( ) = significance level.

Horizon Depth (cm)	Al_e	Al_o	Pret	Fe_p	Al_p	CEC	C	LOI	Fe_o	NaF	Mg	BS_C	pH
0-10	-.98 (.00)	-.96 (.01)	-.91 (.03)	-.90 (.04)	-.89 (.04)	-.88 (.05)							
10-20	-.97 (.00)	-.96 (.01)	-.96 (.01)	-.95 (.01)	-.95 (.01)	-.91 (.03)	-.90 (.03)	-.98 (.00)					
20-30	-.90 (.04)	-.98 (.00)	-.97 (.01)	-.98 (.00)	-.94 (.02)			-.92 (.03)	-.93 (.07)	-.91 (.03)	.89 (.05)	.83 (.08)	
30-40	-.96 (.01)	-.89 (.05)	-.94 (.02)	-.93 (.02)	-.95 (.01)	-.90 (.04)				-.89 (.04)	.89 (.04)		.98 (.00)
40-50			-.96 (.01)		-.93 (.05)				-.96 (.01)	-.91 (.03)			.92 (.03)
50-60													
60-70									-.95 (.02)				.87 (.05)
70-80													.87 (.05)
80-90									-.89 (.04)	-.87 (.05)			.90 (.04)
90-100									-.87 (.05)	-.87 (.06)			.91 (.03)

2.3.4 Variability in fescue tussock morphology, composition and mineral content on T4

To provide basic biological data for a typical undeveloped, grazed, fescue tussock grassland (Chapter 1.5), the fescue population on the main surface at Puffers Stream, T4, was quantitativly investigated. Statistics summarizing the main morphological parameters, nutrient concentrations and their variability, are given in Table 2.11. Eighty one percent of the tussocks on T4 flowered. The largest fescue tussock measured in the study site (on T2) had a maximum leaf length of 78.1 cm, a basal area of 337.3 cm^2 and above ground biomass of 571.0 g DM.

Table 2.11: Morphological and mineral characteristics and variability of fifty-two fescue tussocks on T4

Parameter	MIN	MAX	MEAN	SEM
Basal circumference (cm)	6.3	26.4	14.7	0.8
Longest leaf length (cm)	23.6	48.3	33.9	0.9
Longest flowering culm (cm)	23.0	66.0	38.3	3.0
Live shoot N (mg g^{-1})	9.3	14.9	11.8	0.01
Live shoot P (mg g^{-1})	0.25	0.92	0.62	0.02
Live shoot S (mg g^{-1})	0.44	0.77	0.56	0.02

Frequency distributions of leaf height and basal area were determined from the 400 tussocks used in the biomass regression (Section 2.2.3). Leaf lengths had a distribution closely approximating a normal distribution (Fig. 2.5) while basal area frequency was clearly skewed (Fig. 2.6). Figure 2.7 shows the frequency distribution expressed as $\log_2$ basal area class emphasising the proportion of the small tussocks, the most sensitive indicators of demographic change.

Basal area distribution showed a high frequency of small tussocks with a progressively lower frequency of large individuals (Fig. 2.6). Mathmatical description of the frequency distribution by either negative exponential or power curves depended on the size of the basal area class chosen for grouping frequency. As class size increased (eg from 10 cm classes : 0-10cm, 10-20... to 30 cm classes : 0-30cm,...etc.) the distribution more closely approximated a classical 'reverse-J' distribution (Fig. 2.6) and the equation fit improved (Table 2.12).

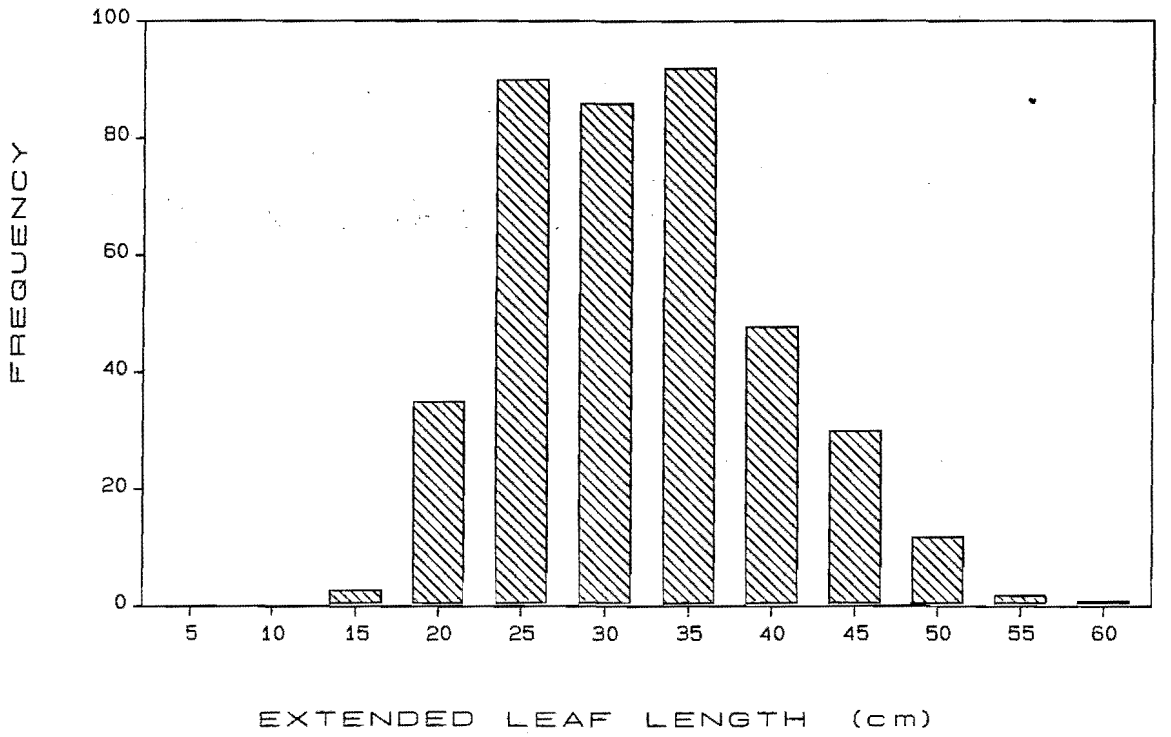


Figure 2.5 : Frequency distribution of fescue tussock leaf length T4

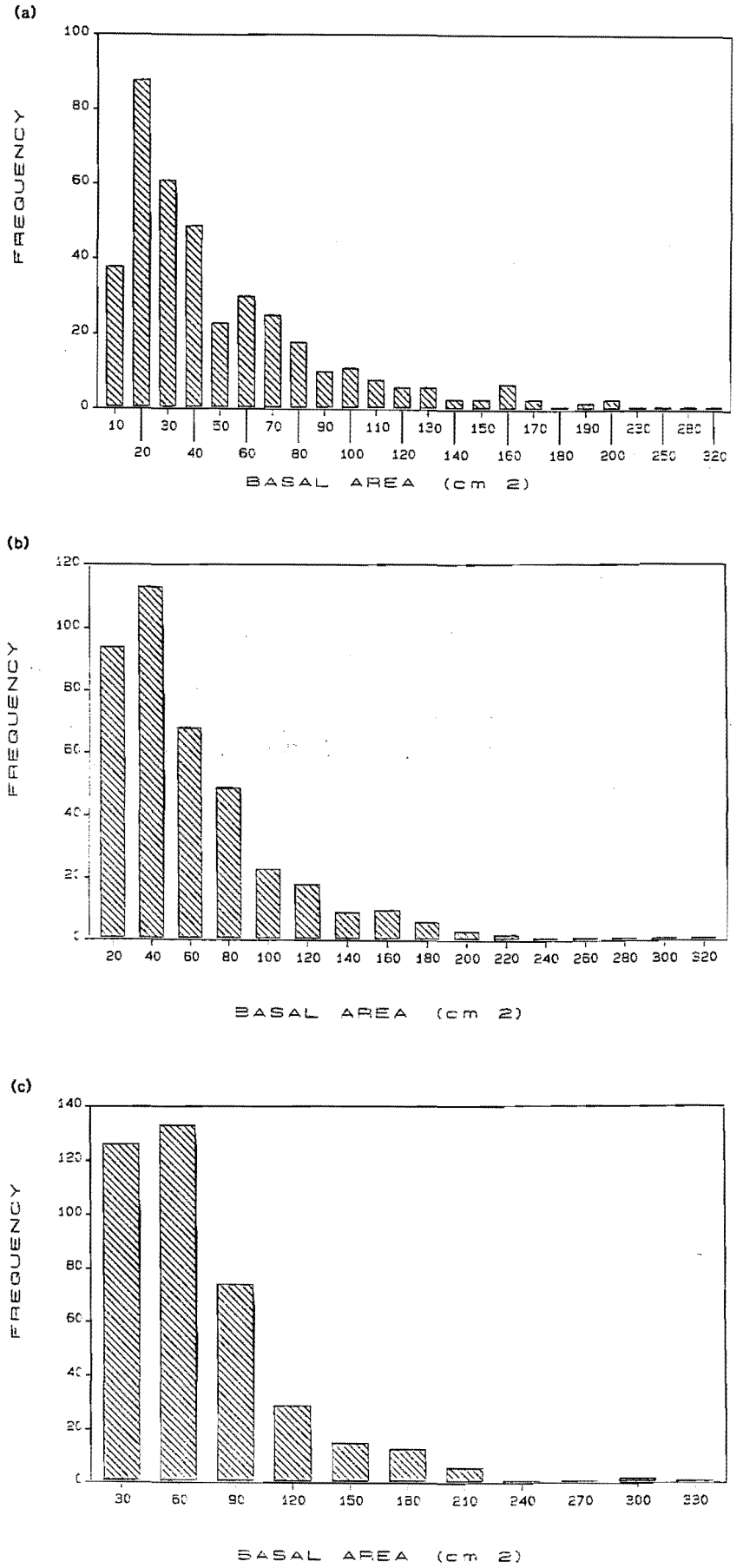


Figure 2.6 : Basal area frequency distribution of fescue tussock on T4 with differing basal area class interval :(a) 10 cm classes (b) 20 cm classes (c) 30 cm classes

Table 2.12: Exponential and power curve equations for basal area frequency distributions with differing class size interval. (r = correlation coefficient)

Basal Class (cm)	Exponential	Power Curve
5	$Y = 22.97 * 0.932^X$ (r = -0.872)	$Y = 131.23 * X^{-1.186}$ (r = -0.873)
10	$Y = 54.53 * 0.857^X$ (r = -0.923)	$Y = 210.68 * X^{-1.470}$ (r = -0.905)
15	$Y = 94.52 * 0.783^X$ (r = -0.958)	$Y = 291.64 * X^{-1.738}$ (r = -0.931)
20	$Y = 147.82 * 0.702^X$ (r = -0.971)	$Y = 397.66 * X^{-2.091}$ (r = -0936)
25	$Y = 189.18 * 0.572^X$ (r = -0.966)	$Y = 392.92 * X^{-2.168}$ (r = -0.934)
30	$Y = 281.41 * 0.572^X$ (r = -0.961)	$Y = 431.63 * X^{-2.377}$ (r = -0.920)

where Y = Frequency and X = Basal area.

Tussock biomass composition and variability on T4 are summarised in Table 2.13. The mean tussock above ground DM was 31.3 g with 23.5 % of the tussock live. The frequency distribution of the percentage of live shoot biomass in tussocks was approximately normal (Fig. 2.8) typical of many biological parameters in natural populations.

Table 2.13 : Mean above ground biomass composition and variability in fifty-two fescue tussocks on T4.

Parameter	MIN	MAX	MEAN	SEM
Live shoot DM (g)	1.0	19.4	6.2	0.6
Live flowering shoot DM (n = 42)	0.3	3.7	1.2	0.1
Recent dead shoot DM (g)	1.4	69.7	15.3	1.4
Old dead shoot DM (g)	0.1	31.2	8.8	1.0
TOTAL above ground DM (g)	2.7	123.3	31.3	3.3
% Live shoot	5.2	45.2	23.5	1.2
% Flowering shoot	0.1	1.0	0.8	-
% Recent dead shoot	26.3	77.3	46.4	1.4
% Old dead shoot	2.3	59.8	29.3	1.8

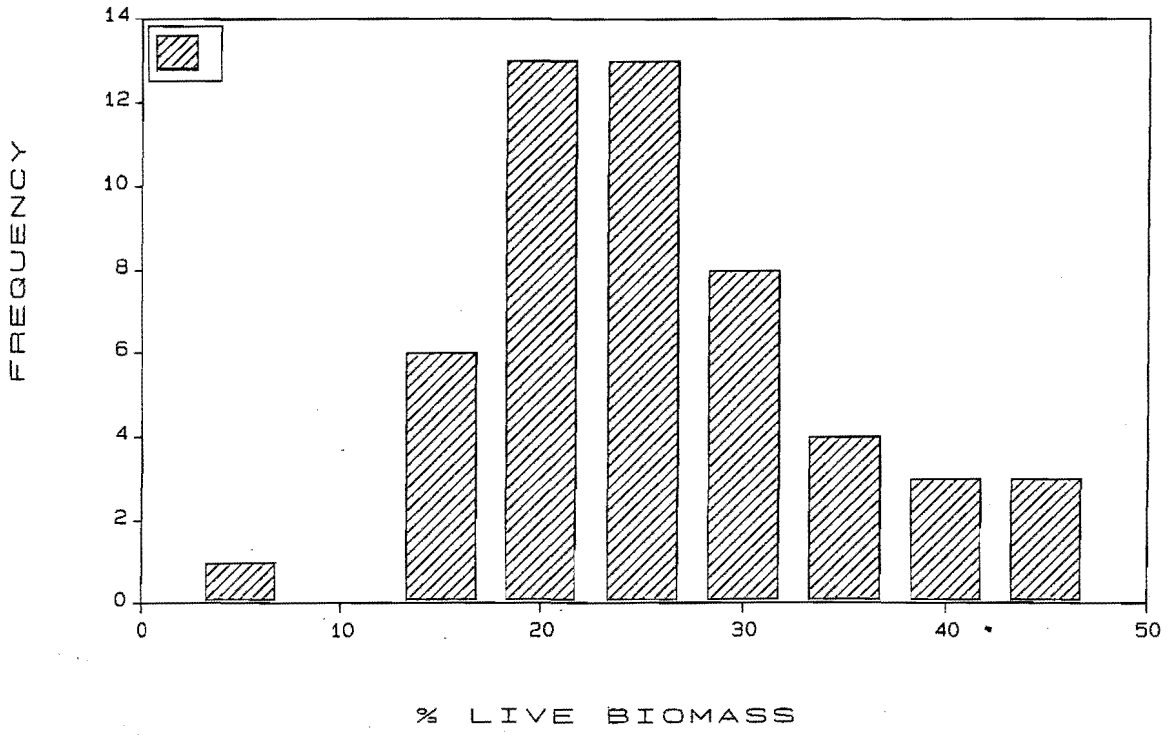


Figure 2.7 : Log $_2$ fescue tussock basal area frequency distribution on T4

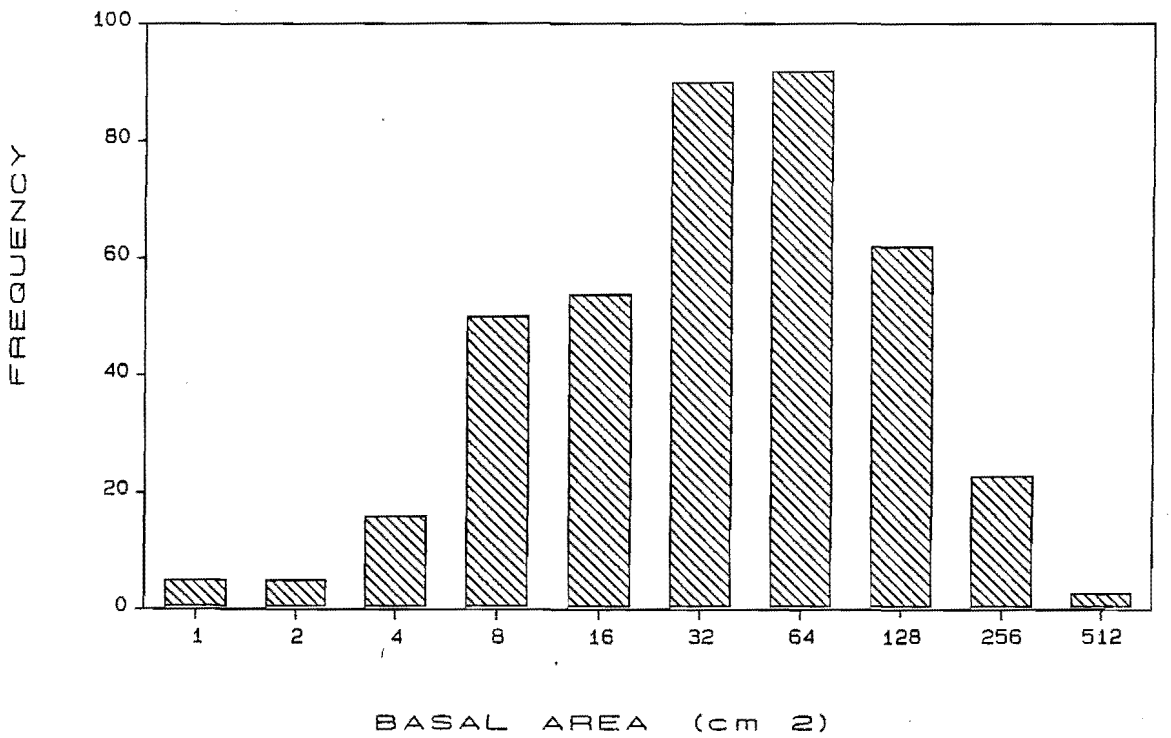


Figure 2.8 : Frequency distribution of fescue tussock live biomass on T4

2.4 DISCUSSION

2.4.1 Estimation of fescue tussock biomass

Field measurement of tussock basal area and leaf length allowed acceptable estimation of total aerial biomass (Section 2.2.4). The regression equations cover the range of most field tussocks and held tolerably well even with unusually large plants. Whether the equations apply generally throughout the fescue tussock grasslands has not been investigated. If they do, then quantification of tussock biomass from easily measured field parameters will be an extremely useful technique for monitoring fescue tussock grassland condition.

2.4.2 Fescue tussock density

There are surprisingly few estimates of fescue tussock density to compare results against considering the extent of the fescue tussock grasslands. Malcolm (1925) recorded a frequency of 'Festuca' (presumably *F novae-zelandiae*) of 1.8 plants per m^{-2} in an ungrazed exclosure at Cass and 2.1 plants m^{-2} outside it. Thornton (1958) reported densities of 9.0 tussocks m^{-2} at both Waiouru and Bealey and between 3.6 to 1.6 tussocks m^{-2} at Alexandra. Density in undeveloped fescue tussock grassland at Pukaki was 2.5 tussocks m^{-2} but varied from 0.4 to 3.3 tussocks m^{-2} under different superphosphate and grazing regimes (O'Connor 1967b). Laycock and Batcheler (1975) made a complete census of fescue tussocks near Cave Stream in two 404.7 m^{-2} plots on a south-west slope at 1040 m elevation. One plot, with a relatively uniform complete cover had a density of 8.9 tussocks m^{-2}; while the other, containing patches of bare ground up to 3 m across, had 3.2 tussocks m^{-2}. Tussock density, averaged across plots through the adjacent Harper-Avoca, catchment was 3.7 plants m^{-2} (Evans, unpublished data). Densities recorded in permanent quadrats at Molesworth were ca. 2.1 - 2.3 tussocks m^{-2} (Moore 1976).

In comparison, the highest density recorded at Puffers Stream, between 11.0-13.6 tussocks m^{-2} on T2 (Table 2.4), appears relatively high for fescue tussock grassland. Density on the main surface, 5.5 tussocks m^{-2} is considerably higher than depleted grasslands though slightly lower than at comparable sites at Craigieburn and Bealey. Accurate fescue tussock density and biomass information is important for providing criteria for judging the relative merit of potential sites for conservation or other uses.

2.4.3 Soil effect on fescue tussock density and size

Correlation of density and basal area with soil parameters was restricted by (a) the limited number of soils available for comparison and (b) only element concentrations rather the total quantities present in the soil being measured. Nevertheless the high correlation of topsoil phosphorus fractions with tussock density strongly suggest P is an important factor influencing density (Table 2.6). Nitrogen may also be important (Table 2.6). The number of fescue tussocks establishing from

seed was improved by N and P application (Dunbar 1970, 1974), thus demonstrating N and P can increase tussock density. Tussock density, however, does not simply depend on mineral nutrition as O'Connor (1967b) has shown : lax grazing with applied P increased tussock density whereas hard grazing reduced densities.

Mean basal area tussock^{-1} increased as topsoil P concentrations increased (Table 2.7). Applied P has been demonstrated to increase fescue tussock DM in pot experiments (Morrison 1958, Dunbar 1974) and also in the field (Dunbar 1974, O'Connor 1961, 1967b). Burrows (1977) attributed the enhanced vigour of tussocks near stock tracks at Cass to nitrogen and phosphorus enrichment via dung and urine. It seems reasonable to conclude therefore that P availability, either through soil inorganic P (appatite Pa) or organic (Porg) pools, is a causal factor determining fescue tussock size.

2.4.4 Soil effect on matagouri density and size

The high matagouri volume on T1 is consistent with its widespread occurrence on young surfaces (Daly 1967, 1969, Hunter 1986). This may be directly due to enhanced nutrient availability, particularly of readily available calcium-bound phosphate (Daly 1969). The high correlation of plant density with subsoil P fractions (Table 2.9) may be evidence in partial support of this view. Matagouri roots penetrate beyond 3 m (Daly 1967, 1969) and the ability to obtain P from unweathered subsoil material may be an important strategy in a P limited environment. The ability of matagouri to extract P from subsoils is presently unknown.

The availability of subsoil moisture may also be a key factor in matagouri growth. This explanation would account for the high aerial volume on T1, adjacent to Puffers Stream,and also the seemingly anomalous increase on T5, the nominally oldest surface (ignoring possible higher P levels from the exposed volcanogenic rock on the western margin of the terrace (Chapter 1.4)). The perched gley horizons in pits close to the sample plots (Chapter 1.4) indicate an impermeable sub-stratum and presumably greater water retention into the summer.

Alternatively the highly significant negative correlations with various extractable aluminium fractions, though notably not with exchangeable aluminium itself, and the strong positive correlation with pH (Table 2.10) may suggest that soil acidity and aluminium may be implicated in matagouri distribution. The highly negative correlation with factors increasing with pedological development, oxalate extractable-Al, organic Carbon and P retention, are consistent with the dominance of matagouri on fresh surfaces, as previously mentioned. What is surprising however, is the low correlation of either density or stature with topsoil P levels. This may be due to the small sample range of five soils or may indicate that factors associated with the negative correlations may *restrict* matagouri to young surfaces rather than a simple causal relationship with high P availability as has previously been suggested (Daly 1967, 1969). This is consistent with the general decrease in matagouri

importance from brown and yellow-grey earths to yellow-brown earths and its occurrence on young surfaces in yellow-brown earths (Hunter 1986).

2.4.5 Field variability in fescue tussock morphology

Variability in morphological characteristics may be due to interaction of edaphic and climatic factors and the inherent genetic plasticity of the particular character (Grime *et al.* 1986). The long flowering culm length on T2 may be due to the high P availability, micro-climate (eg the lower mean wind velocity (Chapter 1.3.2)), or an interaction between these factors. The lower mean leaf length on T4 relative to other terraces (Table 2.5) is puzzling. It may reflect sampling since the mean leaf length of the 50 tussocks sampled for variability measurement on the same surface was higher (33.9 vs 26.9 cm). The longer leaf lengths on T1 might possibly reflect enhanced N supply via transfer from matagouri (Chapter 3). Further investigation of edaphic influences on tussock variability follows (Chapters 3 and 4).

As with density, there is very little published data available regarding the morphological characteristics of fescue tussock populations throughout New Zealand. The Puffers Stream tussock data allows objective comparison with values reported by other workers and provides quantitative critera for ecological interpretation.

The mean leaf length on T4, 38.8 cm (Table 2.5) is almost exactly the mid point of the 30.5 to 45.7 cm range in leaf length reported at Cass by Malcolm (1925) but slightly longer than Sewell's 32.0 cm average leaf length elsewhere in the Waimakariri (Sewell 1947, 1952) . It is also longer than the 26.2 cm mean value from plots throughout the adjacent Harper-Avoca catchment (Evans unpub. data) and the 30.5 and 20.3 mean height reported for Waiouru and Bealey grasslands (Thornton 1958).

Similarly, the longest flowering culm length at Puffers Stream (66.0 cm) is almost identical to the 64.3 cm recorded on Sewell's large tussocks and the 63.5 cm measured by Connor (1963) at the Kowai river, below Porters Pass. The mean basal circumference of 14.7 cm on T4 is very close to the 18.8 cm mean circumference obtained from averaging Sewell's (1947) large and small tussock circumferences from Cass, Craigieburn and Grasmere. It is considerably higher than the 2.3 cm^2 measured at Waiouru by Thornton (1958).

Thus it appears that the Puffers Stream tussocks are morphologically similar to tussocks elsewhere in the Waimakariri. At present, ascertaining the significance of the differences between fescue tussock populations from other areas is difficult due to limited knowledge regarding sampling and site factors. Future quantitative studies however, will be able to be rigorously compared against the Puffers Stream data, if desired.

2.4.6 Fescue tussock population structure

The highly skewed basal area frequency distribution on T4 is typical of many plant populations (Harper 1977, Meyer 1952, Wardle 1984). However the frequency of small fescue tussocks is lower than expected in a population with continuous recruitment and growth (see Wardle 1984). This is evident in Fig. 2.6 and particularly in Fig. 2.7 where the log frequency distribution emphasizes the smaller classes. The expected distribution under continuous recruitment to the population is a linear decrease in frequency with increasing basal area class (Batcheler 1986). This contrasts the notably fewer small tussocks up to 16 cm^2 basal area at Puffers Stream (Fig 2.5).

There are three possible explanations:

(1) Small individuals were incorrectly censused.
(2) Small individuals were suppressed by plant competition.
(3) Small individuals had been removed by grazing.

While it is probable that the number of small individuals was underestimated, as fescue tussock can be extremely small and inconspicuous (Moore 1976) and small individuals in close proximity to larger plants may have been incorrectly lumped, the difference is too great to be attributed to incorrect recording. Plant competition could be responsible for suppression (Harper 1977) and Dunbar (1970, 1974) has shown that although increased cover initially improved fescue seedling survival, the competition decreased long term survival and growth.

It is more likely the absence is directly related to the greater vulnerability of fescue plants to grazing where small. The grasslands at Puffers Stream have been grazed annually since early 1850's (McLeod and Burrows 1977, McLeod 1977). Cockayne (1916) comments that seedling tussocks were readily grazed though mature plants were ignored. Hughes (1975) found mature tussocks were not apparently selected for grazing by sheep but did not comment on seedlings. Rabbits will graze fescue tussock (Cockayne 1916, Moore 1976) though rabbit populations in the Waimakariri have never been high (Malcolm 1925, Sewell 1947).

Similar depressions in the expected frequency distributions occur with palatable forest species e.g. *Coprosma* species, *Nothofagus solandri var cliffortioides* but not less palatable plants e.g. *Pseudowintera colorata, Nothofagus menziesii* and are directly attributable to browsing (Wardle 1984, Batcheler 1985, 1986). It is therefore extremely probable this explanation also applies at Puffers Stream.

The available evidence shows the local Waimakairi fescue tussock populations are being maintained under grazing (Malcolm 1925, Sewell 1947, 1952, Moffat 1956). This infers the low seedling levels are adequate for tussock replacement or longevity and clonal fragmentation may be important mechanisms for maintaining site occupancy (cf Moore 1977).

2.4.7 Fescue tussock biomass and nutrient content

The standing crop of fescue tussock on T1-T5, ranging between 1,250 - 2,500 kg ha^{-1}, is greater than the 560 kg ha^{-1} reported for a severely modified fescue tussock grassland at 1050 m in the Craigieburn Range near Cave Stream (Evans 1980). However the percentage of live biomass, 22%, is lower than the 39% at Craigieburn although almost identical to the 23.5% live leaves in tussocks elsewhere in Waimakariri Valley fescue grasslands (Sewell 1947). The greater percentage of live biomass on the Craigieburn range may be due to higher precipitation (Chapter 1-3) and the greater exposure to north west winds at Puffers Stream, though this is merely conjecture.

The total live biomass. ranging from 275 - 550 kg ha^{-1} on T1-T5, is higher than the 210 kg ha^{-1} recorded on the Craigieburn Range (Evans 1980). In comparison with tall tussock grassland the upper level of live shoot DM at Puffers stream is approximately a tenth that of live *Chionochloa rigida* shoots at Paddle Hill creek in Ashburton (6660 kg ha^{-1} Williams 1977) and the 6600 kg ha^{-1} reported by O'Connor and Powell (1963) for the same species at Mackenzie Pass. The fescue values are, however, comparable with similar North American sub-alpine prairie grasslands. For example, the closely related species *Festuca idahoensis* has an above ground live biomass of 2,450 kg ha^{-1} in the Olympic mountains Washington (Kuramota and Bliss 1970). Mean live biomass was slightly higher than comparable African grassland sites in the Serengeti (McNaughton 1985).

The low green blade N and P concentrations in fescue tussock at Puffers Stream confirm the results of Coop *et al.* (1953). Nitrogen and P concentrations are 1.3 and 3.3 times higher than those in fescue tussock from the Craigieburn Range (Evans 1980) but whether this is due to lower availability and/or greater competition from adventive species at Craigieburn is not clear.

In comparison with other widespread indigenous New Zealand grasses, N concentrations in fescue tussock are 1.2-1.5 times higher than in tall tussocks *(Chionochloa)* species; P 5-7 times higher and S 4-8 times higher (Connor *et al.* 1970, Williams *et al.* 1977 1978, Payton *et al.* 1986). Phosphorus concentrations are 5-7 times higher than in the low-fertility tolerant sweet vernal (*Anthoxantum odoratum*) on strongly developed greywacke soils (Wells 1956a, 1956b, Wells and Saunders 1960). The average N concentration in fescue tussock is 3 times lower than in the high-fertility pasture grass ryegrass (*Lolium perenne*) while P and S are about 2 times lower (McNaught 1970).

Thus fescue tussock appears an intermediate, moderate to low-fertility grass, maintaining higher tissue nutrient concentrations than low-fertility adapted grasses but lower tissue nutrient concentrations than high-fertility adapted grasses.

2.5 CONCLUSIONS

Quantitative description of fescue tussock in a typical undeveloped fescue tussock grassland at Puffers Stream, on the main surface, T4, was as follows : mean leaf length was 33.9 cm, ranging from 23.6 to 48.3 cm, flowering culm height averaged 38.3 cm, ranging from 23.0 to 66.0 cm, and basal area 14.7 cm^2 ranging from 6.3 to 26.4 cm^2.

Tussock above ground biomass averaged 30.7 g DM ranging from 3.2 to 98.2 g DM. The average composition was 24 % live, 1 % live flowering, 46 % recently dead and 29 % old dead shoot DM. Total above ground biomass per unit area ranged from 1,250 to 2,500 kg DM ha^{-1} with total live biomass ranging from 280 to 570 kg DM ha^{-1}. These values are similar to other short tussock communities in the Waimakariri and alpine meadows in North America.

Mineral concentration in live shoots for nitrogen averaged 11.8 mg g^{-1} DM, ranging from 9.3 to 14.9 mg g^{-1}; phosphorus averaged 0.62 mg g^{-1} DM, ranging from 0.25 to 0.92 mg g^{-1} DM and sulphur averaged 0.56 mg g^{-1}, ranging from 0.44 to 0.77 mg g^{-1} DM. These values are slightly higher than in grasses adapted to very infertile soils but low compared to pasture grasses. Fescue tussock thus appears to best be classed as a low-fertility tollerant grass.

Frequency distribution of tussock basal area showed a high frequency of small tussocks decreasing to a low frequency of large tussocks. Description by negative exponential and power curve equations depended on the size of the basal area class interval used for calculating frequency and therefore appeared to have limited biological validity.

The frequency of small fescue plants was lower than expected in a naturally recruiting population, probably due to grazing. This suggests tussock longevity and clonal spread by fragmentation may be important mechanisms for maintaining site occupancy.

On a development sequence of five soils, T1-T5, fescue tussock density ranged from 3.2 to 11.2 tussocks m^{-2}. These densities are comparable or higher, than in other New Zealand fescue grasslands. Densities were greatest on the soils with the highest topsoil phosphorus concentrations suggesting that P availability may be an important factor determining fescue density. Nitrogen may also be influential. Matagouri, a co-dominant shrub on T1-T5, had densities varying from 0.8 to 1.6 plants m^{-2} and was positively correlated with subsoil P fractions.

Fescue production on T1-T5, assessed as basal area, was closely correlated with topsoil phosphorus whereas matagouri production, measured as aerial volume, was strongly negatively correlated with oxalate-extractable aluminium, P retention and organic carbon but was not significantly correlated with soil P fractions. Causal factors determining matagouri distribution and growth are probably high nutrient supply (particularly P, possibly from subsoil sources) and subsoil moisture. Limited tolerance to factors associated with soil maturity, e.g. aluminium toxicity, may

restrict matagouri to young surfaces as soil parameters such as oxalate-extractable aluminium were strongly negatively correlated with aerial volume.

These results are consistent with the hypothesis that both fescue tussock and matagouri growth decrease as pedological development increases but fescue tussock is less affected by soil infertility.

CHAPTER 3: SEASONAL VARIATION IN MINERAL COMPOSITION OF *FESTUCA NOVAE-ZELANDIAE* ON THREE HIGH COUNTRY YELLOW BROWN EARTH SOILS.

3.1 INTRODUCTION

Precise determination of plant available nutrients and their influence in determining species abundance or growth is a central problem in soil-plant relationship studies (Asher and Edwards 1983, Moorby and Besford 1983, Schultz and Chapin 1987). Chemical assessment of soil nutrient status, as used in the previous chapter (Section 2.3), may not necessarily reflect true availability or causal relationships (Greig-Smith 1983, Gigon 1987). Furthermore a single assessment of soil fertility may be misleading as nutrient levels fluctuate and plant uptake during nutrient flushes may be critical for plant nutrition in infertile habitats (Chapin 1980, McSweeny 1983). Chemical analysis of plant tissue concentration and derivation of nutrient uptake have long been used to assess more directly the biological availability of nutrients (Goodall and Gregory 1947, Bouma 1983).

This chapter continues the investigation of *Festuca novae-zelandia* edaphic ecology by monitoring tussock nutrient concentrations. There were two objectives:

1. To compare nutrient supplying power with increasing pedological development.

2. To determine seasonal changes in mineral concentration in *Festuca novae-zelandia.*

3.2 METHODS

Ten tussocks were sampled monthly or bimonthly on three terraces spanning the range of pedological development at Puffers Stream, T1, T3, T5 (Chapter 1.4) using a modified point-transect method (Levy and Madden 1933, Stone 1962). The nearest tussock to a boot every third pace on a transect across each terrace was sampled providing it had more than 25 live tillers. If a tussock had fewer than 25 live tillers the balance was obtained from the nearest neighbouring tussock. The transect origin varied in each sampling period. Tillers were bulked per surface in 1981 but were bulked from every two tussocks in 1982, giving five samples per surface to assess variability. Tillers were immediately taken to Lincoln College and stored in a deep freeze (- 3.0 °C) until they were prepared for analysis. Sampling dates in 1981 were: 4 February, 3 March, 23 March, 1 May, 29 May, 2 July, 29 August, 11 October and 19 November and in 1982 on 20 January, 6 March, 29 April, 19 June, 4 August, 4 September, 2 November and 20 December.

After thawing, live and dead tissues were fractionated as follows. Leaves were arbitrarily defined as live if more than 20% of the lamina was green and live and dead leaves were separated for each tiller. Leaves were cut off by scalpel at the base of the sheath. Blades were separated at the ligule from mature sheaths and from immature sheaths at the change in colour of the lower basal portion. The youngest undifferentiated

sheaths were not separated from the blade. Dead blade tips were cut off at the junction with living tissue. Where there was a gradient of senescing material, separation was made half way between clearly live and clearly dead tissue. Flowering culms were cut off at the sheath junction or, where indistinct, arbitrarily at the diffuse junction between buff base and green blade. Inflorescences were separated from the culm at the base of the panicle.

Foliage fractions were dried in a forced draught oven for 24 hours at 70-100 °C and weighed ± 0.01 g. Blade and tip fractions were then ground for 30 seconds in a Tema mill to pass a 0.5 mm sieve and analysed for macro-elements as specified in Appendix 2.3.

Statistical analysis used the ANOVA procedures outlined in Chapter 2.2.

3.3 RESULTS

3.3.1 Shoot Mineral Composition

Differences in N and P concentration in green blades were highly significant for both month and terrace ($p < .001$). Nitrogen concentrations were consistently higher on T1 than the other terraces (Fig. 3.1). There was little difference between T3 and T5. Seasonal patterns were similar on all three terraces with peak concentration in late winter-spring.

The seasonal pattern of blade P concentration was generally similar to N, excepting October and November 1981 (Fig. 3.2). While P concentrations on T1 were very similar to those in T3, they were consistently lower on T5 ($p < .001$). Blade N:P ratios showed no obvious seasonal pattern (Fig. 3.3) but the mean ratios, 8.1 on T1, 5.6 on T3 and 7.4 on T5 differed significantly ($p < .001$).

In contrast, sulphur availability seemed similar in all terraces (Fig. 3.4). The exceptionally high value for T3 in November may be an analytical error: there appears no good biological reason for the increase on this terrace but not on the others. Unfortunately no sample remained for re-analysis. Excluding this value there appeared to be little difference in monthly S concentrations in blades.

As expected, N and P concentrations in dead tip tissue were always less than in corresponding blade tissue (Fig. 3.5). Tip N concentration relative to blade was always higher than the same ratio for P though the seasonal pattern for the two minerals was almost identical.

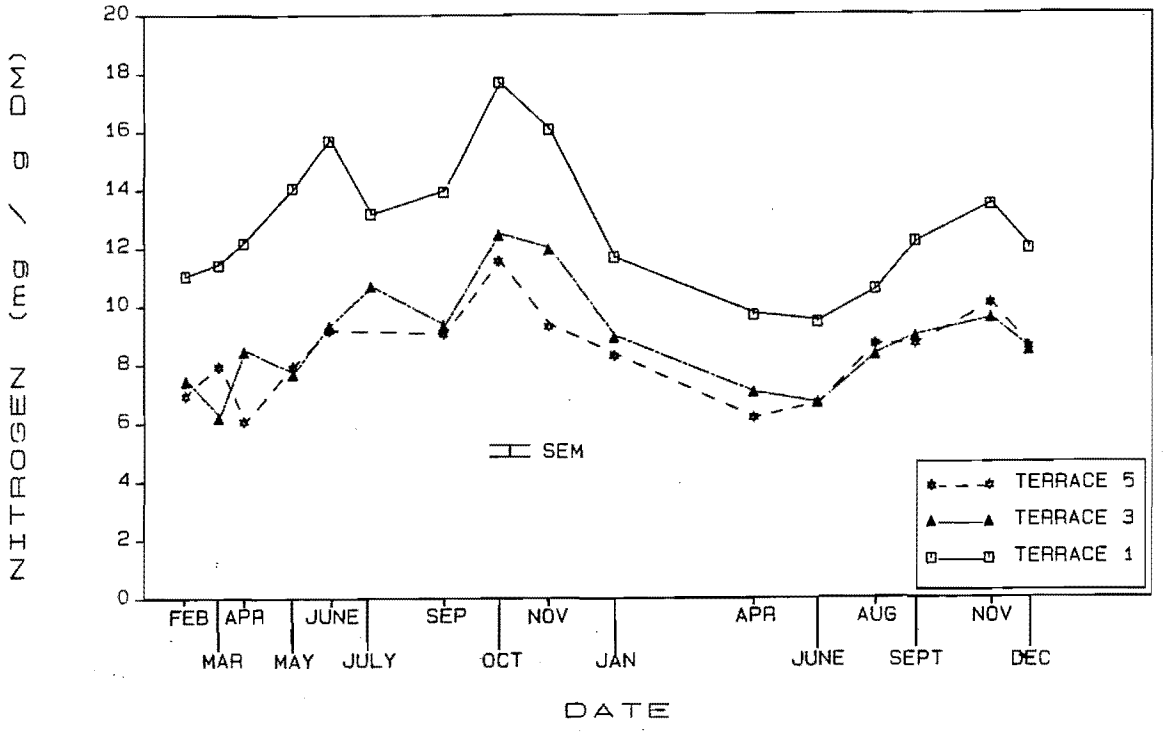


Figure 3.1 : Seasonal variation in live blade N concentration 1981 -1982.

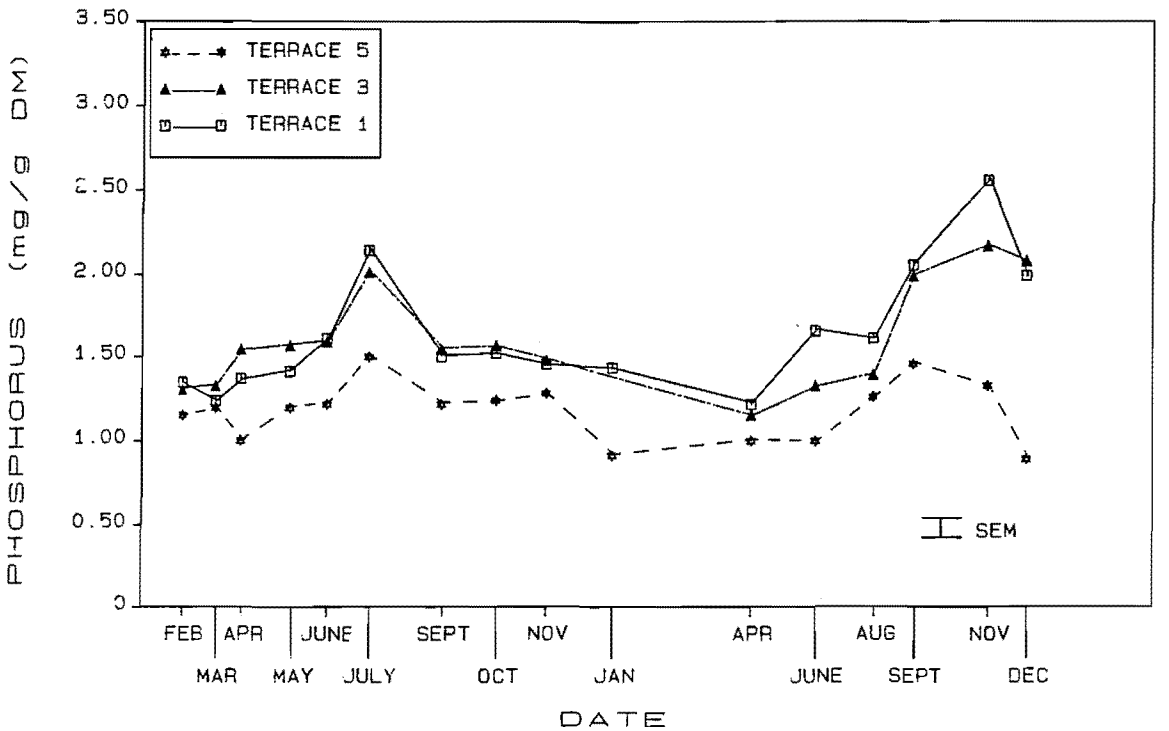


Figure 3.2 : Seasonal variation in live blade P concentration 1981 -1982.

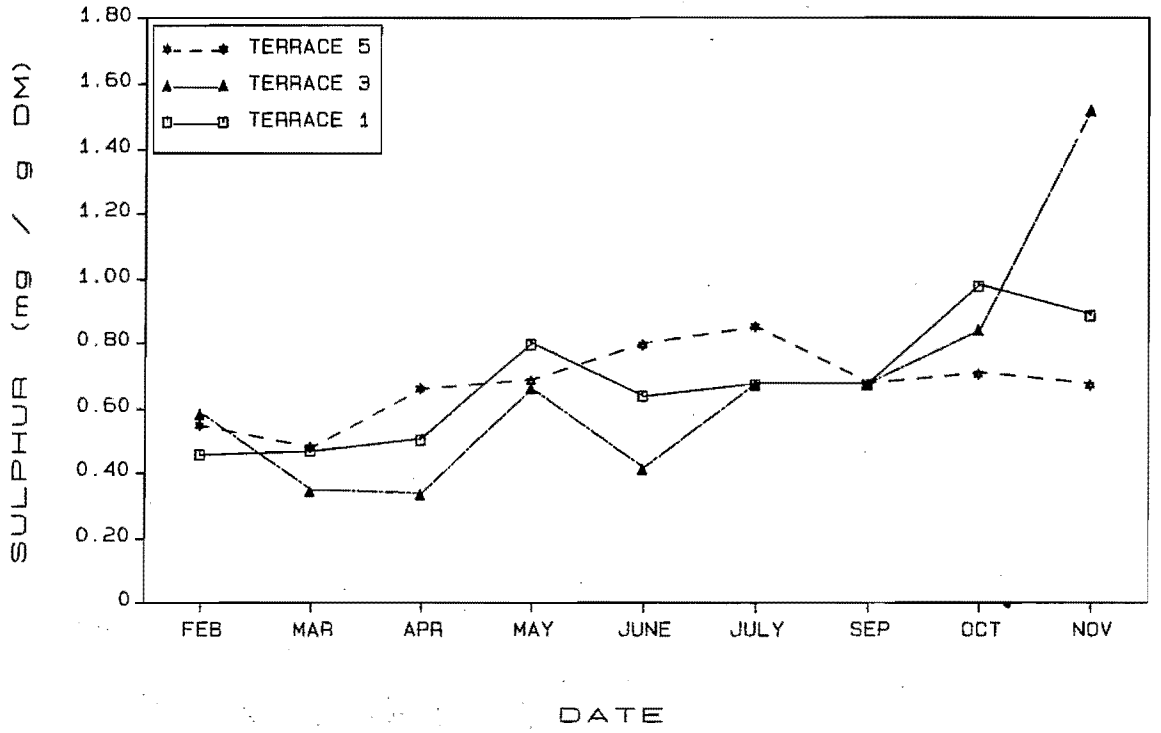


Figure 3.3 : Seasonal variation in blade S concentration 1981 -1982.

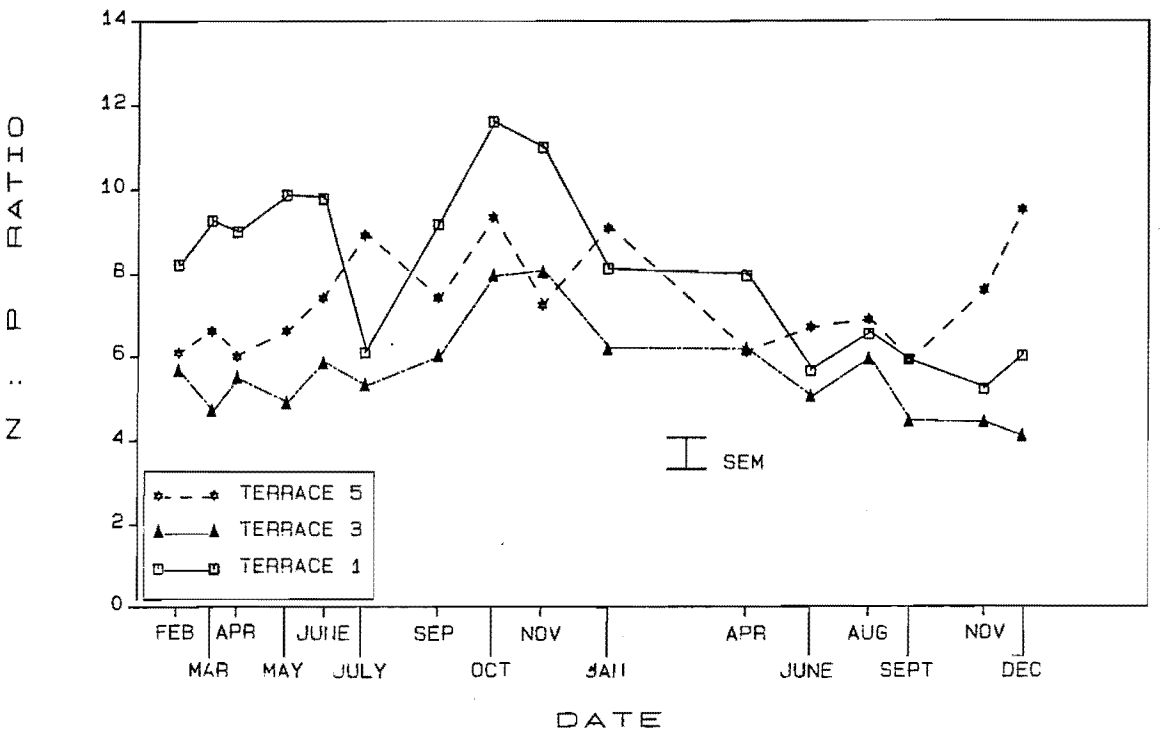


Figure 3.4 : Seasonal variation in blade N:P ratios 1982-1983

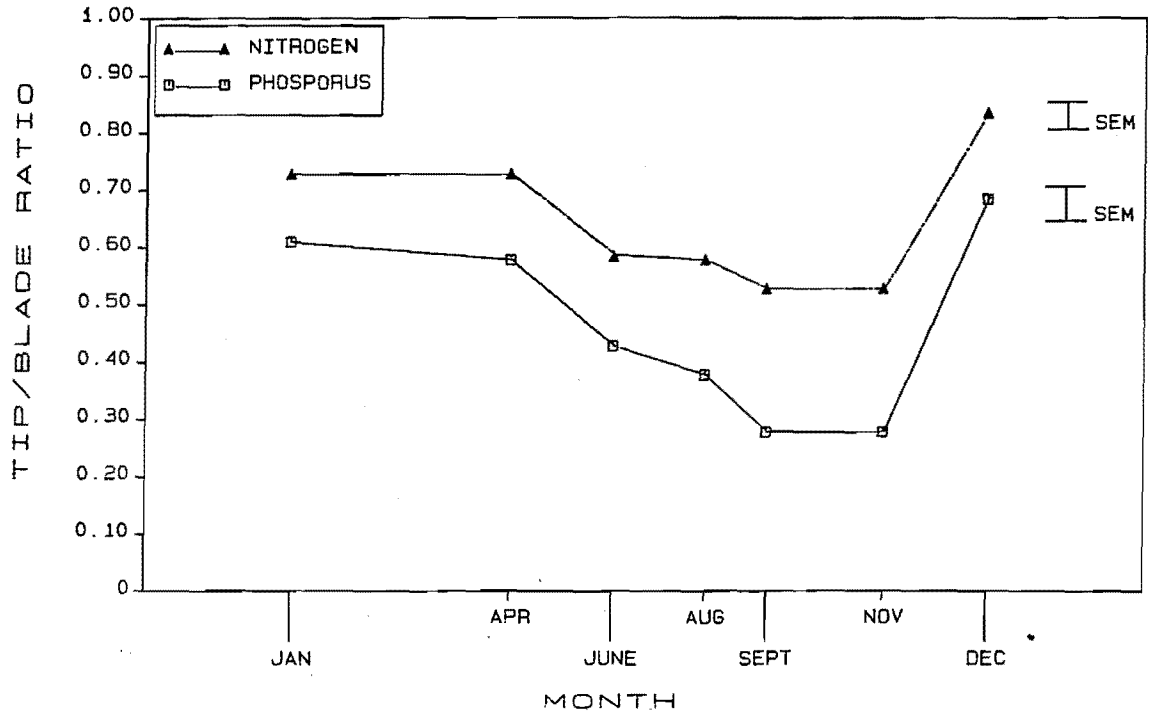


Figure 3.5 : Seasonal variation in dead tip N and P concentrations 1981-1982.

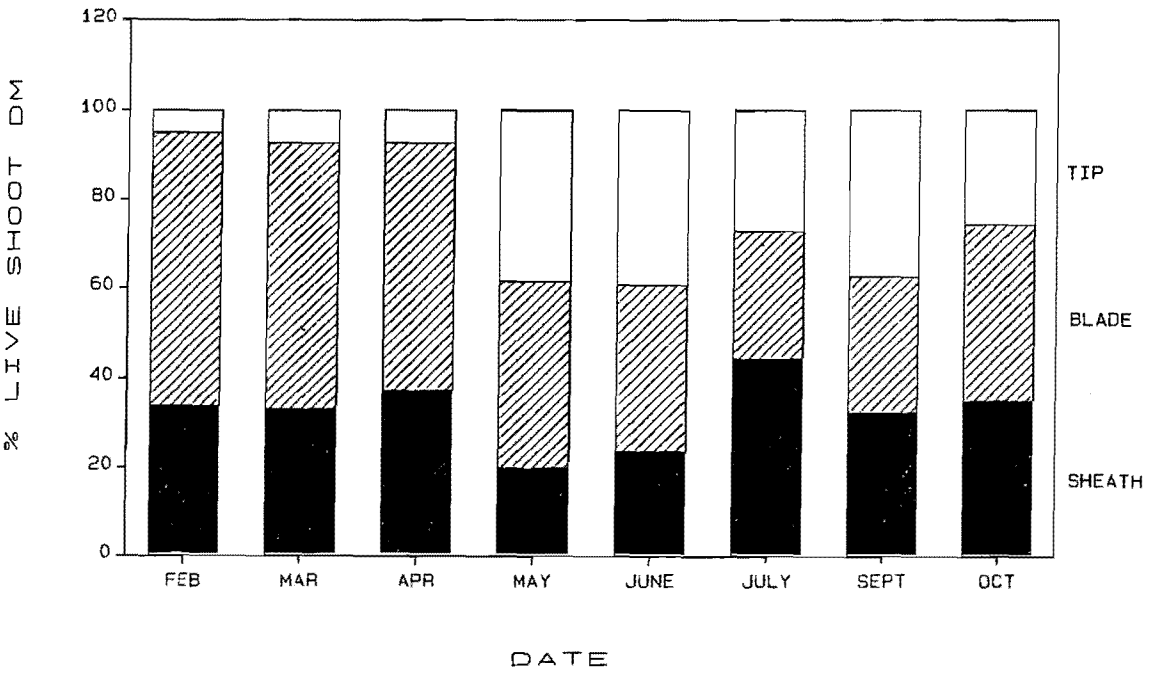


Figure 3.6 : Seasonal variation in shoot composition 1981.

3.3.2 Shoot Biomass Composition

Seasonal variation in live shoot biomass composition was highly significant ($p < .001$). The proportion of dead tip increased sharply in winter with a simultaneous decrease in sheath weight (Fig. 3.6).

3.4 DISCUSSION

The seasonal fluctuation in green blade N concentration, between a summer minimum and winter-spring maximum (Fig. 3.1), is very similar to the seasonal pattern occurring in pasture grasses (Johns 1955, McNaught and Dorofaeff 1968, Metson and Saunders 1978b, Reay and Waugh 1983). The main difference, the maintenance of high tissue N concentration into late spring, is consistent with the shorter growing season in the high country.

The lowest N concentrations, in summer, occurred in the period of maximum growth rate in vegetative and flowering shoots (Sewell, 1947). The increase in N concentration in May - June 1981 on T1 may be synchronous with the surge in soil organic matter mineralization and increased ammonium and nitrate levels observed by McSweeny (1983) in winter in tall tussock grasslands. The effect did not occur on T3, T5 or in 1982 so may possibly be only a sampling artifact.

Furthermore the increase in N and P over winter suggests fescue tussock may have the ability to obtain and sequester nutrients during periods of low plant growth. This strategy is advantageous for slow growing species in infertile environments where nutrient flushes occur (Grime 1979, Grime and Hunt 1975, Chapin and Bloom 1976, Chapin et al 1978, Chapin 1980).

Nitrogen availability was clearly greater on T1, though not appreciably different between T3 or T5 (Fig. 3.1). This may explain the longer leaf length on T1 (Chapter 2.3) as N promotes leaf growth (Moorby and Besford, 1983).

The enhanced N status of T1 is consistent with its postulated early successional stage (see Stevens 1968, Stevens and Walker 1970) and presumably has resulted from transfer from the N fixed by matagouri. Matagouri growth on this terrace was considerably greater than on the other terraces (Chapter 2.3) and it seems reasonable to infer this also applies to N fixation.

Seasonal fluctuation in P concentrations peaked in July 1982 and in November in 1982 (Fig. 3.2) with a summer-autumn minimum. The spring increase is similar to pasture grasses (Fig. 3.2; Saunders and Metson 1971, 1978a, Reay and Marsh 1976, Reay and Waugh 1983). The variation between seasons is not immediately explicable but may

be related to release of P from soil organic residues and organic matter (Metson and Saunders, 1971).

Terrace five was clearly lower in P supplying power than the other two terraces, which did not differ appreciably (Fig. 3.2). This is consistent with the lower growth on T5 relative to other terraces (Chapter 2.3, 7.3, 9.3) and suggests P deficiency is probably a primary factor limiting growth.

The determination of plant available P is in good agreement with the expected availability from topsoil chemical values for the three terraces (Table 8.4). The decrease from T3 to T5 is consistent with P availability decreasing as pedological development increases (Walker and Syers 1976). The anomalously low P availability on T1, less than expected for a young soil (Walker and Syers 1976), is probably due to incorporation of pre-weathered material (see Harrison and Swift 1984). The high N:P ratios on T1 (Fig. 3.3) therefore reflect the greater N concentrations on T1 relative to T3. In contrast, the lower P concentrations on T5 relative to T3 are responsible for the higher N:P ratios on T5.

The lack of any consistent seasonal difference in sulphur concentration (Fig. 3.4) is also consistent with results from North Island soils (Metson and Saunders 1978a). The similarity in sulphur concentrations on T1, T3 and T5 suggests that S supply does not appear to be a major factor influencing growth between terraces.

Season variation in shoot components (Fig. 3.5) is similar to variation in tall tussock (Mark 1965, Williams 1977). In *C. rigida* at Paddle Hill Creek, Ashburton, the dead tip fraction decreased from 32.1% of the shoot in October to 10.5% in March before increasing to 23.1% in September (data calculated from Fig. 28 in Williams 1977). This is similar to the pattern at Puffers Stream excepting the smaller percentage contribution of the tip fraction from February through to April (5-8%) with a major increase in May to 23%. The increase is coincident with the sharp drop in mean air temperatures below freezing point (Fig. 1.16) and strongly suggests frosting is responsible for the rapid increase in dead tip tissue. As new shoots begin to elongate from October onwards they progressively lower the contribution of dead tips to the shoot biomass pool.

The sudden decrease in sheath weight in May and June is probably an experimental artifact due to the death, and hence removal from the live shoot sample, of the previously outermost living leaf. This removed the oldest mature sheaths and as the inner sheaths are not proportionally as large, relative to blades, this would result in the observed decrease. There was no similar decrease in *Chionochloa* sheaths (Williams 1977).

3.5 CONCLUSION

The nutrient supplying power of soils, assessed by monitoring fescue tussock tissue nutrient concentrations for two years, were broadly consistent with levels expected from pedological development. Terrace one, the youngest soil, was highest in plant available nitrogen and terrace five, the oldest soil, was lowest in plant available phosphorus. P availability on T1 was lower than expected, probably indicative of incorporation of pre-weathered material in the solum. Sulphur availability appeared similar on all terraces.

Fescue tussock green blade N concentrations increased significantly to a spring maximum and decreased to a summer minimum. Phosphorus followed a similar pattern in 1982. Blade sulphur concentrations showed no consistent seasonal trends.

The proportion of distal dead blade tissue in live shoots sharply increased from 5-8% in summer and autumn to 20% in winter, attributed to frosting.

CHAPTER 4: GROWTH AND MINERAL COMPOSITION OF TRANSPLANTED *FESTUCA NOVAE-ZELANDIAE* ON FIVE HIGH COUNTRY YELLOW BROWN EARTH SOILS.

4.1 INTRODUCTION

An ultimate objective of plant ecological investigation is to generate hypotheses about the relationship between vegetation and environment (Grieg-Smith 1985). As early as the 1920's Clemment and Goldsmith (1924) advocated using plants experimentally to directly measure environment. Individuals of uniform age, size, history and, if using clonal material, genetic composition, could be transplanted into undisturbed natural populations. The effects of the environmental factors affecting the plant are integrated in its growth, morphology, physiological status and reproductive behaviour (Harper 1977). There has recently been renewed interest in use of this technique (Turkington *et al.* 1979, Antonovics *et al.* 1987).

To further investigate the environmental factors responsible for differences in resident fescue tussock populations (Chapter 2), but with greater experimental control, cloned tussocks were transplanted into the development sequence of the five Puffers Stream terrace soils (Chapter 1.4).

4.2 METHODS

Twenty fescue tussocks on terrace four (T4), immediately due north of T5, were removed with a 5 cm root turf to Lincoln College on 6 January 1981. Each tussock was fractionated into single or double tiller ramets and planted in a heated sandbox in a automatic mist-spray glasshouse by 16 January.

In August healthy, well rooted ramets from each clone line were transferred to sand-potting mix flats prior to transplanting. In late September the flats were removed from the glasshouse to acclimatize.

In October about 400 ramets, maintaining the clone lines, were graded on tiller size and root vigour. All dead tillers and leaves were removed and 100 ramets, ranging from 3 to 10 tillers per ramet were selected and tagged with coloured plastic coated wire according to the number of tillers present. Fifty-five ramets had between 3 to 6 tillers: the remainder between 7 to 10. The longest leaf length was measured ± 0.2 cm (Chapter 2.3).

Twenty ramets per terrace, with similar tiller numbers between terraces, were planted on the 22 October. Clone lines were systematically allocated between terraces but randomised within a terrace.

Ramets were positioned in a standardized rectangular pattern of four ramets 20 cm apart in a row with 40 cm between rows. Planting blocks were chosen to avoid proximity to resident tussocks or matagouri. Vegetation was principally brown top (*Agrostis tenuis*), sweet vernal (*Anthoxanthum odoratum*) and *Raoulia subsericea* (and on T4 *Coprosma petrieii*).

The experimental design was a random block with the five terraces the main treatment and five blocks with four replicates per block on each terrace. Statistical analysis

used the ANOVA procedures outlined in Chapter 2.2.5. Tiller numbers differed significantly between terraces at planting ($p < .05$) so adjustment by co-variance analysis was made for the number of tillers originally present on all subsequent analyses.

Six months later, at the end of the first growing season (5 May 1982), the number of live, dead and flowering tillers were recorded. The count was repeated the following spring (24 October 1982) and all plants were harvested at ground level at the end of the second growing season (24 April 1983). Plants were transported to Lincoln College and deep frozen at - 6 °C within three hours.

After thawing, the number of dead, live and flowering tillers were recorded including remnant stumps remaining from detached dead tillers. The number of live and dead leaves, defined as previously (Chapter 3.2), were counted and the length of the longest leaf and longest live leaf were measured as before (Chapter 2.2).

Live leaves were separated into live shoot (sheath plus blade) and dead blade tip (cf Chapter 2.2). All other dead matter was pooled. Fractions were dried in a forced draught oven for 24 hrs at 65-70°C and weighed ± 0.02 g. The live shoot and dead tip fractions were separately ground to pass a 1 mm sieve and analysed for macronutrients as described in Chapter 6.2.

4.3 RESULTS

Eighty two of the 100 transplants survived by the end of the first growing season (5 May 1982). This dropped to 80 after the first winter (5 October 1982) and to 77 by the following autumn 24 April 1983; Table 4.1). Mortality did not differ significantly between terraces ($p < .50$).

Table 4.1: Number of dead ramets from 100 transplanted fescue tussock ramets on T1-T5 1981-1982.

Date	TERRACE				
	1	2	3	4	5
5/5/1982	6	2	4	0	5
5/10/1982	6	3	4	1	5
28/4/1983	6	3	7	2	5

Tiller numbers increased on all terraces after transplanting with a clear difference between T1 and all other terraces (Fig. 4.1). By 18 months this difference was highly significant ($p < .001$).

The number of live tillers, though they did not differ significantly by the end of the experiment, showed more variation between terraces than the total number of tillers (Fig. 4.2).

Leaf production, also adjusted by covariance analysis on the number of tillers originally present, was significantly higher on T1 relative to other terraces ($p < .006$). The proportion of living leaves ($p < .001$) and longest live leaf length ($p < .02$) were also significantly higher on this terrace (Table 4.2).

Table 4.2: Leaf number, length and percentage live T1-T5 30 months after transplanting.

	TERRACE					
	1	2	3	4	5	SEM
Leaf number	103.2	64.4	63.3	59.5	61.5	8.9
% Live leaves	36.8	28.5	23.5	32.4	29.7	2.1
Longest live length (cm)	26.3	17.4	21.5	19.2	17.1	1.7
Longest length (cm)	31.0	29.9	29.9	26.8	30.0	1.7

Shoot dry matter, similarly adjusted by co-variance analysis to correct for initial differences in ramet size, differed significantly between terraces in live shoot ($p < .03$) and dead tip ($p < .001$) but not total DM (Table 4.3).

Table 4.3: Shoot dry matter components 30 months after transplanting T1-T5 (g).

Shoot	TERRACE					
Component	1	2	3	4	5	SEM
Live blade & sheath	.28	.16	.19	.18	.14	.04
Dead tip	.05	.03	.02	.02	.02	.01
Dead shoot	.53	.51	.59	.50	.48	.06
TOTAL	.86	.70	.80	.71	.64	.10

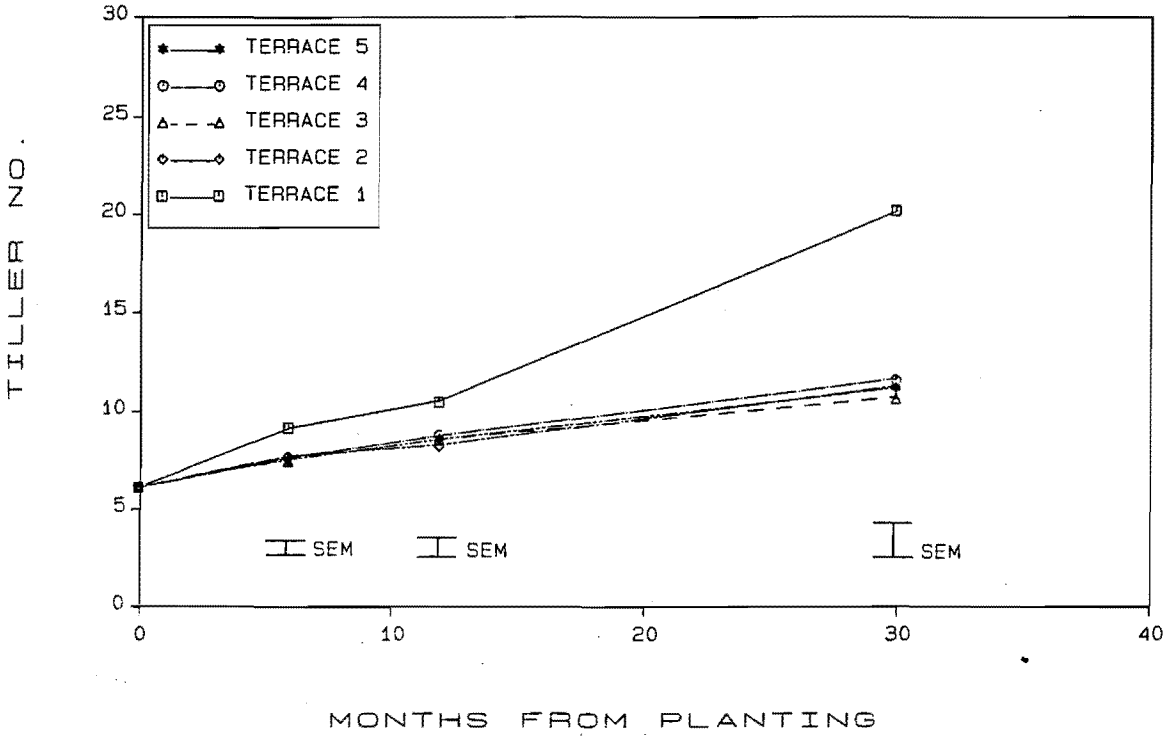


Figure 4.1 : Total number of tillers in transplanted fescue tussock ramets on T1-T5 .

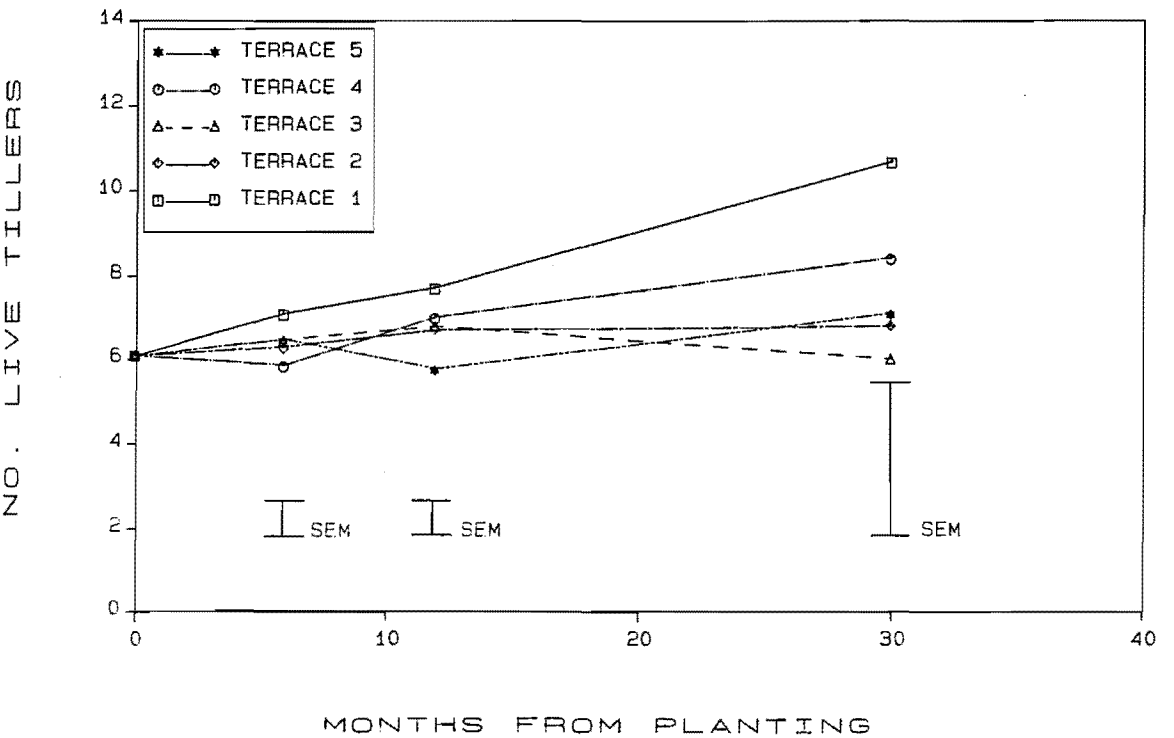


Figure 4.2 : Total number of live tillers in transplanted fescue tussock ramets on T1-T5 .

The relationship between number of tillers and leaves with total dry matter was curvilinear and $\log_e$ transformations gave the best fits:

$$DM = 0.103 + 0.312 \log_e \text{ Tiller No.} \qquad r = .608$$

$$\log_e DM = -2.77 + 0.700 \log_e \text{ Leaf No.} \qquad r = .619$$

Correlation analysis of co-variance adjusted live and total DM with 30 soil chemical variables (see Appendix 2.2) showed highly significant correlations with factors associated with soil acidity (Table 4.4). Dry matter was positively correlated with pH and subsoil base cations but negatively with exchangeable aluminium and hydrogen. The rapid increase in exchangeable aluminium levels with decreasing pH is shown in Fig. 4.3.

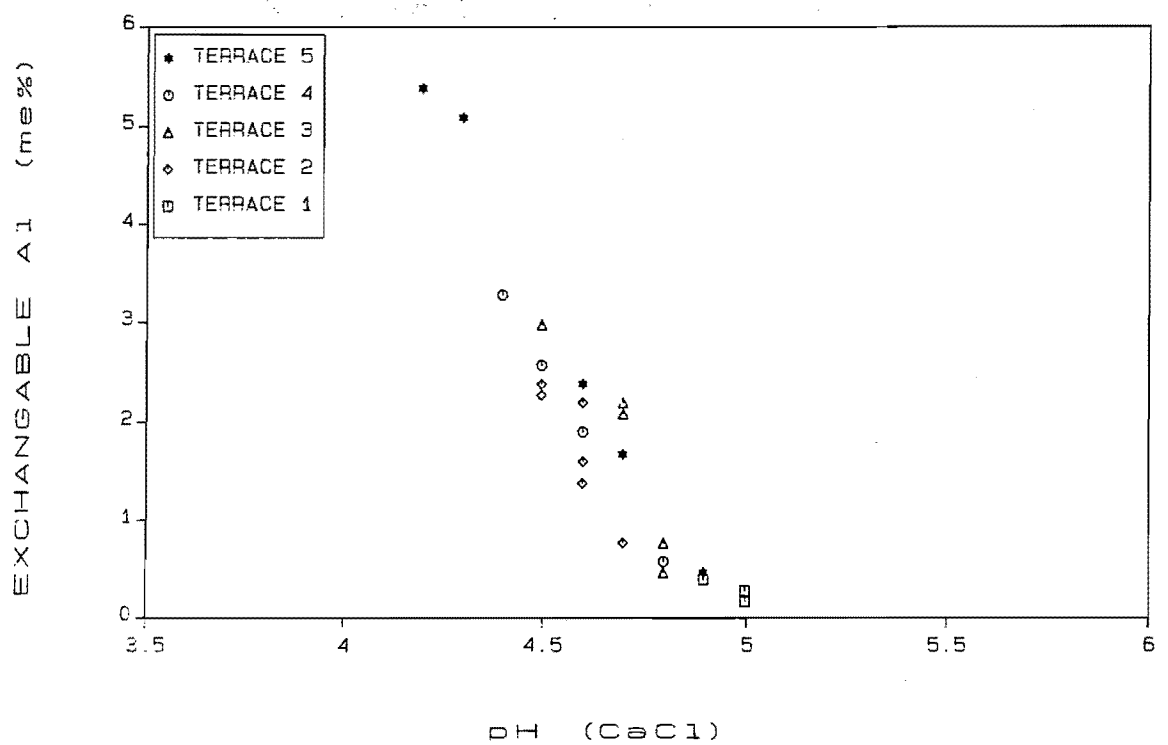


Figure 4.3 : The relationship of exchangable Al and soil pH on T1-T5 .

Table 4.4: The most highly correlated Soil chemical parameters 10-40 cm depth with total transplant DM after 30 months. Pearson correlation coefficient r; (significance probability).

Horizon Depth	Si_o	pH	Soil pHCl	Parameter H	Al	Bs_e	Fe_e
10	**.92** (.03)	.76 (.14)		-.86 (.06)			
20			**.91** (.03)		-.85 (.06)		**-.88** (.05)
30			**.99** (.00)	-.80 (.10)	**-.89** (.04)		
40			**.94** (.02)		**-.98** (.00)	.83 (.08)	

Live shoot N and P tissue concentrations differed significantly between terraces ($p < .001$). Nitrogen levels were markedly higher on T1 relative to other terraces and P concentrations highest on T4 and T2 and lowest on T5 (Table 4.5). Concentrations in blade dead tips, as expected, were lower than in live shoots though the proportion retained in tips varied strikingly between terraces (Table 4.5).

Table 4.5: Nitrogen and phosphorus concentrations in live shoot and dead tip tissue T1-T5 30 months after transplanting (mg/g DM).

Fraction	TERRACE 1	2	3	4	5	SEM	p
Shoot N	12.91	7.31	6.91	8.81	7.04	5.7	***
Shoot P	1.36	1.83	1.64	1.92	0.91	0.9	***
Tip N	6.07	5.95	-	4.04	2.43	-	-
Tip P	0.46	0.75	-	1.09	0.21	-	-
Tip N /Blade N	0.47	0.81	-	0.46	0.35	-	-
Tip P /Blade P	0.34	0.41	-	0.57	0.22	-	-

Total N uptake was significantly higher on T1 compared with the other terraces ($p < .001$). Terrace 4 was also higher in available N and P and T5 clearly lower in both elements compared with T2 and T3 (Fig. 4.4).

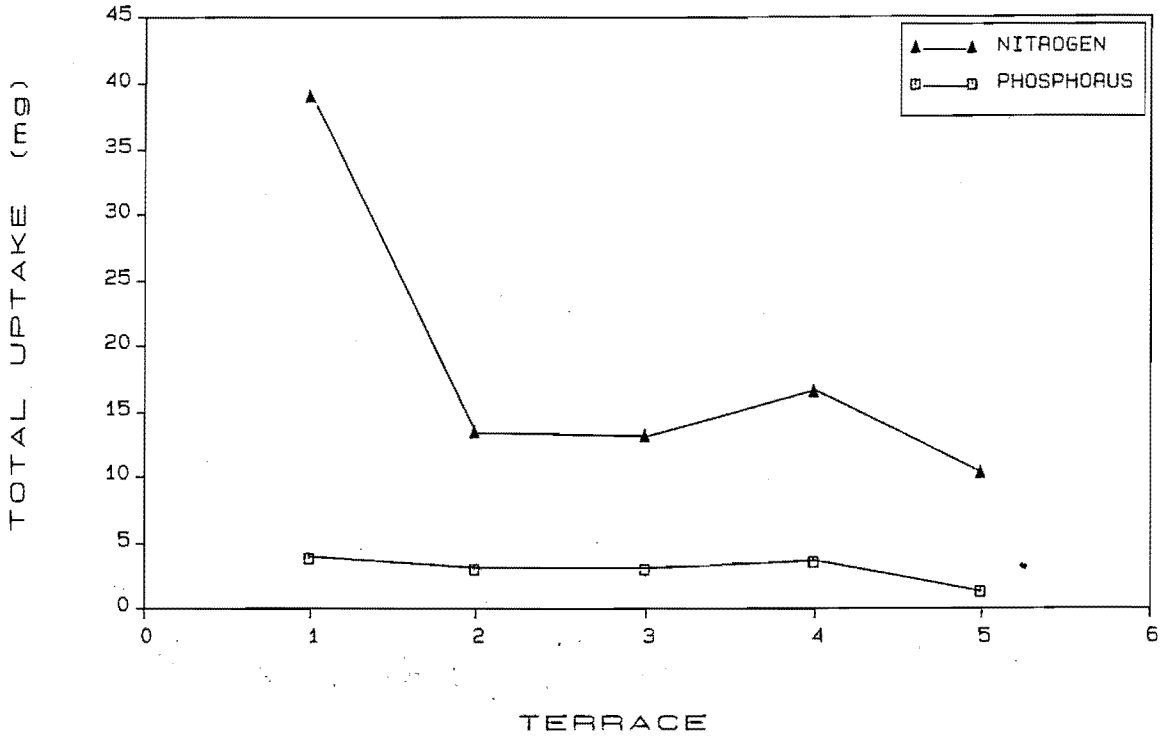


Figure 4.4 : Total N and P uptake in transplanted fescue tussock ramets on T1-T5 .

Transplanted ramet growth and mineral concentration on T1 - T5 were very similar to undisturbed natural tussocks (Chapters 2 & 3). Morphology, compared as mean leaf length and biomass, was closely related in the two experiments (Figs. 4.5, 4.6):

Field LTH = -18.9 + 1.70 Tspt. LTH r = .899

Field DM = -24.6 + 60.4 Tspt. DM r = .832

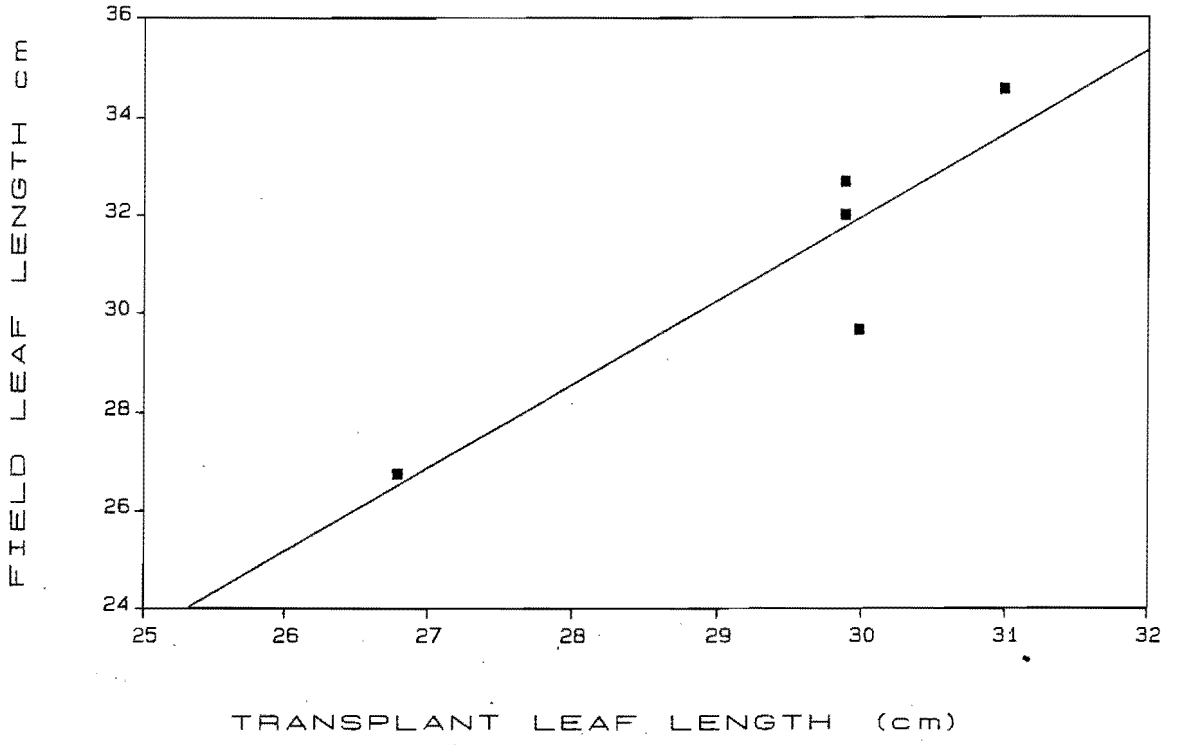


Figure 4.5 : The relationship between leaf length in transplanted and natural fescue tussock on T1-T5 .

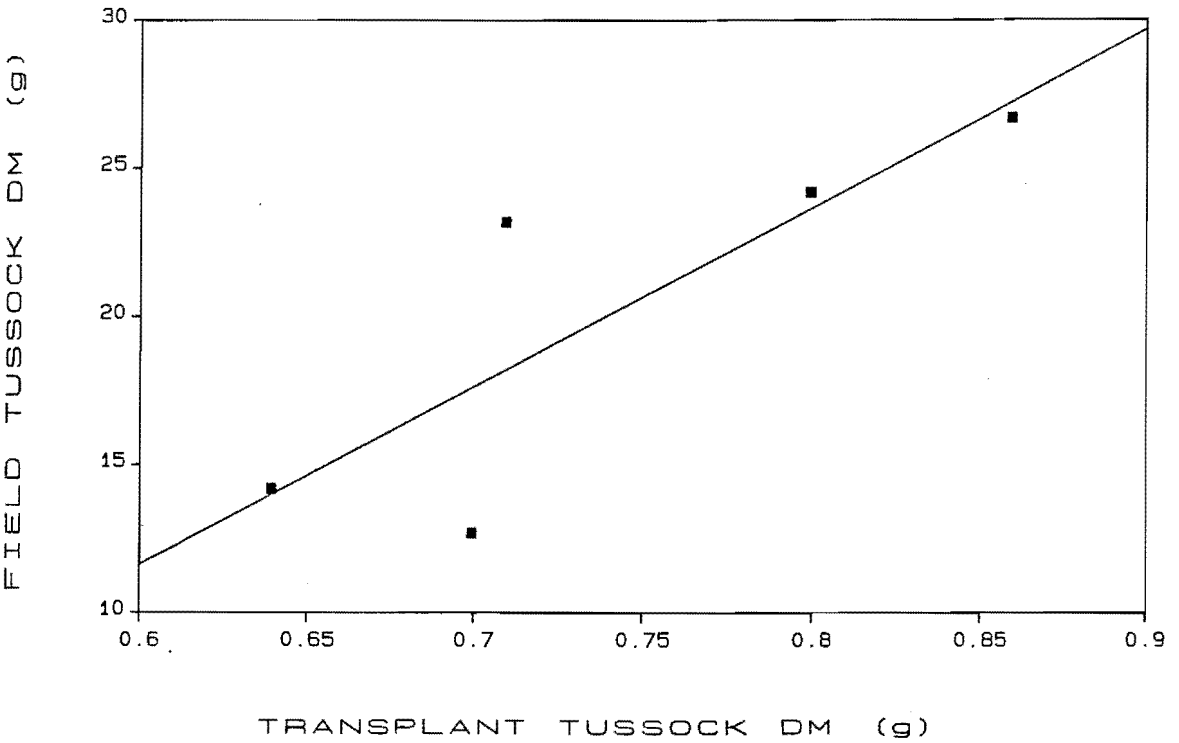


Figure 4.6 : The relationship between transplanted and natural fescue tussock above ground biomass on T1-T5 .

Live shoot N and P concentrations in transplants, were reasonably similar to concentrations in natural tussocks, averaged over two years (Chapter 3), on the same terrace (Table 4.6).

Table 4.6: Nitrogen and phosphorus live shoot tissue concentrations in field and transplanted fescue tussocks (mg/g DM).

TERRACE	Nitrogen		Phosphorus	
	Field	Tspt.	Field	Tspt.
1	12.8	12.9	1.6	1.4
3	8.9	6.9	1.6	1.6
5	8.7	7.0	1.2	0.9

4.4 DISCUSSION

The high initial transplant mortality during the first summer (Table 4.1) was probably due to the abnormally low rainfall, particularly during February and March 1982. Precipitation was 75 - 100% below the long term normal for the area (Chapter 1.3.3). Consistent with this is the highest mortality occurring on T1, the soil with the lowest water holding capacity due to its coarse texture (Chapter 1.5). Puffers Stream dried up and topsoil moisture contents, determined gravimetrically, were extremely low, 8 - 10% by weight (unpresented data).

The close relationships between size, morphology and mineral content of transplanted and natural fescue tussocks (Figs. 4.5, 4.6; Table 4.6) demonstrate the differences observed between natural tussocks on T1-T5 (Chapters 2 and 3) are not due to localised genotypic specialisation on each terrace. This also shows it is reasonable to extrapolate between behaviour of ramets and natural tussocks - an assumption fundamental to the pot experiments in the next chapter.

Micro-climate is unlikely to be responsible for the differences in transplant growth on T1-T5. Growth on T2, only 20m and 2m higher from the T1 transplants (Chapter 1), was considerably lower than on T1 (Fig. 4.3; Table 4.2, 4.3) but differed little from more exposed upper terraces. It is more probable differences in growth are principally determined by edaphic factors, though water availability from Puffers Stream may have had some effect, particularly during establishment.

Factors associated with acidity were the soil variables most closely correlated with transplant growth (Table 4.4). Soil acidity is a principal factor controlling pastoral production in high country soils (Grigg 1981, Sinclair and McIntosh 1983) and pH and exchangeable aluminium (Al) were two of the three soil factors responsible for explaining the highest proportion of variation in ryegrass (*Lolium perenne*) and white clover (*Trifolium repens*) yields across the entire range of New Zealand genetic soil groups (Scott and Groves 1982). Soil acidity was also the most important factor responsible for differentiating calciole and calcifuge species in Europe (Rorison 1960, Gigon 1987).

Acidity (pH) is an often merely an index for a complex range of soil factors. Hydrogen ion concentration itself often appears to have a relatively minor effect on plant growth relative to secondary factors: aluminium, manganese and heavy metal solubility, phosphorus availability, cation availability, nitrification and mineralization rates of organic matter (see Schmehl *et al.* 1950, Epstein 1972, Andrew *et al.* 1973, Foy and Wheeler 1979, Haynes and Swift 1986). In many instances Al toxicity alone appears to be the predominant factor (Fox 1979, Bache and Crook 1981, Bollard 1983) or the toxicity is due to the interaction of Al with other elements, particularly phosphorus and calcium (Munns 1965a,b, Clarkson 1966b, Jackson 1967, Foy *et al.* 1973, Heylar 1978, Robson and Pitman 1983).

The effects of Al toxicity in *Gramineae* are well established; e.g. in wheat, barley and rye (Foy *et al.* 1965, Clarkson 1966b, Kerridge *et al.* 1971, Aniol *et al.* 1980). corn (Clark 1977, Rhue *et al.* 1978) sorghum (Furlani and Clark 1981) oats (Alam and Adams 1979) and low fertility grasses such as kikuyu grass (Awad *et al.* 1976) and *Agrostis* species (Clarkson 1966a).

In view of such evidence, the strong negative correlation between fescue tussock biomass and exchangeable Al (Table 4.4) is likely to reflect a causal relationship. Pratt (1969) suggested that levels of soil exchangeable Al above 1.0 milli equivalents percent (me %) are likely to be toxic to sensitive species. Exchangeable Al levels reached 5.4 me% on T5 and exceeded 1.0 me% on every terrace except T1 (Fig. 4.3). Even though fescue tussock is undoubtedly Al tolerant, as demonstrated by growth even on the most acidic surface, it seems reasonable to infer that Al is at least partly responsible for the observed differences in growth.

However the precise mechanisms of aluminium toxicity remain unclear. Whether the low production on T5 is due to direct action of Al in metabolic disruption limiting root growth or function (Bollard 1983), or indirectly by restricting root development to the upper Ah horizon and thus increasing summer moisture stress and/or restricting the volume of soil available for exploitation is unknown. Whether the low T5 shoot tissue P concentration (Table 4.5) or uptake (Fig. 4.4) is due to the lower P status of the soil or is due to Al inhibition of P uptake cannot be determined from this experiment.

It is also unclear whether the increase in tussock DM with higher base saturation levels (Table 4.2) indicates that base cation supply is an important co-factor in the mineral nutrition of fescue tussock. Other results (Chapter 5) suggest cation supply has a relatively minor effect on growth.

The significantly higher leaf and live biomass production on T1 (Fig. 4.1, Table 4.3) is thus likely to be due to lower levels of aluminium (Fig. 4.3) and higher nutrient levels (Table 1.6) relative to other terraces.

Nitrogen is probably the primary factor responsible for the superior growth on T1 as its uptake was almost twice that on other terraces (Fig 4.4). The effect of increasing nutrient supply, particularly N, in promoting greater CO_2 assimilation is well established (see Schultz and Chapin 1987). Higher levels of nutrients also changed assimilate partitioning towards higher leaf production rates in *Lolium* and *Festuca* grasslands (Lonsdale and Watkinson 1983).

Although P uptake was also highest on T1 (Fig. 4.4) it was only slightly higher than on T4 and only 25% greater than on T2 and T3. As the differences in growth were considerably greater than differences in P (Fig. 4.1) the main P effect is likely to be through interaction with the high levels of N available on T1. Morrison (1958) demonstrated that fescue tussock response to N accompanied by P was 2- to 4- times the response to either element alone.

The higher biomass of transplanted tussocks on T1 relative to other terraces, when matagouri was absent, contrasts the results from natural populations (Chapter 2.3). This supports the hypothesis (Chapter 2.4) that matagouri competition may be a factor responsible for the size of fescue tussocks on T1.

Interpretation of internal nutrient cycling between shoot pools is restricted because (a) low tip sample weights precluded replication necessary to assess variability within tussocks on a particular terrace and (b) because of the loss of T3 experimental data (Table 4.5). Nevertheless, as in field tussocks, (Chapter 2) it appears that P recovery from dead tips is higher than N. The lower N and P concentrations in T5 tips relative to shoots compared with other terraces may indicate fescue tussock is able to alter internal translocation rates for more efficient nutrient conservation on less fertile sites.

4.5 CONCLUSION

Transplanted fescue tussock growth, morphology and mineral concentrations were closely related to those of natural tussocks occurring on the same terrace. Live biomass, tiller and leaf number were significantly higher on the youngest terrace compared with other terraces. Edaphic rather than microclimatic differences appear to be the causal factors.

Soil acidity was highly correlated with mean transplant biomass on the five terraces. Exchangeable aluminium, significantly negatively correlated with biomass, appeared directly responsible for restricting growth. At low aluminium levels, nitrogen uptake on T1 was twice that on other terraces and, in combination with an adequate supply of phosphorus and other nutrients, suggests nitrogen availability was primarily responsible for the superior tussock growth on this surface.

CHAPTER 5: GROWTH AND MINERAL COMPOSITION OF *FESTUCA NOVAE-ZEALANDIAE* ON FIVE POTTED HIGH COUNTRY YELLOW BROWN EARTH SOILS.

5.1 INTRODUCTION

Harper (1977), discussing the dangers of generalizing about the ecological properties of a species commets:

'There is no meaningful way in which a study made of one sample from a species can be said to represent that species until the range of variation within and between its populations has been established.' (p.751).

By this criterion, examination of mineral nutrition in *Festuca novae-zelandiae* is inadequate. The most comprehensive paper (Morrison 1958), only two and a half pages long, gave no details regarding the fescue tussock used (presumably from a single population at the Bealey site) nor was any statistical assessment made of the difference between treatments. The tussock responded to phosphorus (P) with nitrogen (N) interacting strongly to further increase growth but only small additional responses when sulphur (S) and potassium (K) were included. O'Connor (1967a, 1967b) found N and P fertilisers affected field growth of fescue tussock, yield, basal circumference and leaf length. Scott (1970), using two populations, showed fescue tussock had a low relative growth rate when compared with seven widespread indigenous and naturalized grasses (only *Chionochloa rigida* and *C. rubra* were lower). He also showed, though with a single population, that fescue tussock was the least affected by reduction in nutrient supply. There were only two treatments and 12 pots. Dunbar (1974) reported similar results for fescue tussock from an single population in an experiment effectively reduced to 8 pots: tiller number and shoot weight with N plus P were significantly greater than controls. M^{c}kenzie (1978) provided biochemical data that showed, on re-analysis, highly significant differences between four populations of fescue tussock. P application in this experiment significantly decreased leaf sclerenchyma (O'Connor pers. comm.).

These investigations have demonstrated fescue tussock to be a slow growing, low-fertility tolerant species that responds to nutrient amendment, particularly N and P. There has been no rigorous evaluation, however, of the relative effects of various nutrients nor their interaction. No comparitive information is available regarding growth on different soils or on the interaction between nutrients and soil. Nor has intraspecific edaphic variability been examined.

The pot experiments described in this chapter, in addition to duplicating and extending field studies (Chapters 3 and 4), seek to rectify some of these ommissions. Seven soils, spanning most of the pedological range encountered in the fescue grasslands, were chosen and the effects of N, P, calcium (Ca), magnesium (Mg), K and S, examined. Two fescue populations, drawn from the extremes of the mid Waimakariri precipitation gradient (Chapter 1.3) were used. Results therefore should have reasonable generality for much of the montane fescue tussock grasslands on greywacke derived soils in the eastern South Island.

5.2 MATERIALS AND METHODS

5.2.1 Experimental Design

(a) Soil-Phosphorus-Basal Experiment

The experimental design for the main experiment was a 2x2x2x7 factorial randomised block with:

2	Fescue populations	a) Craigieburn b) Puffers Stream
2	Phosphorus levels	a) 0.0 kg P ha^{-1} b) 100.0 kg P ha^{-1}
2	Basal levels	a) 0.0 b) 50.0 kg K + 20.8 kg Mg + 25.4 kg Ca + 47.9 kg S ha^{-1}
7	Soils	a) 2 Craigieburn Soils CB1, CB4 b) 5 Puffers Stream Soils T1-T5

There were three replications per treatment giving a total of 168 pots.

Three accessory experiments examined the effect of:

(I) Basal fertiliser rate.
(II) Basal fertiliser supplied as sulphate or chloride salts.
(III) Nitrogen fertiliser.

These experiments were factorial extensions of treatments in the main experiment with some pots in common.

(b) Basal Fertiliser Rate Experiment

The experimental design was a 2 x 4 factorial with two levels of P and four levels of basal fertiliser. Phosphorus rates were 0 and 50.0 kg P ha^{-1} and basal rates zero, half, the same and twice the rate used in the main experiment (Table 5.1). There were three replicates per treatment giving a total of 24 pots, 12 pots being common with the main experiment.

Table 5.1: Elemental rates applied in Basal fertilisers (kg ha^{-1}).

Element	0 x	1/2 x	1 x	2 x
Ca	0.0	12.7	24.5	50.8
K	0.0	25.0	50.0	100.0
Mg	0.0	10.4	20.8	41.6
S	0.0	24.0	47.9	95.8
Cl	0.0	22.0	44.1	88.2

The experimental technique was identical to the main experiment except only soil T4 and tillers from the Craigieburn population were used. The experiment was planted on 11 April 1982, three days after the main experiment and run synchronously.

(c) Basal Fertiliser Composition Experiment

The experimental design was a 2 x 2 x 3 factorial with:

2	Soils	(a)	Craigieburn CB4
		(b)	Puffers Stream T4
2	P levels	(a)	0.0 kg P ha^{-1}
		(b)	100.0 kg P ha^{-1}
3	Basal levels	(a)	No Basal
		(b)	Basal as sulphate salts
		(c)	Basal as chloride salts

There were three replicates per treatment giving a total of 36 pots, 24 pots being drawn from the main experiment. The elemental composition of the basal treatments were: kg ha^{-1}:

	Rate (kg ha^{-1})				
	K	Mg	Ca	S	Cl
a) No Basal	0.0	0.0	0.0	0.0	0.0
b) Basal Sulphates	50.0	20.8	25.4	47.8	44.1
c) Basal Chlorides	135.8	50.0	25.4	0.0	323.3

(d) Nitrogen Fertiliser Experiment

The experimental design was a 2 x 2 x 2 x 2 factorial with:

2	Soils	(a)	Craigieburn CB4
		(b)	Puffers Stream T4
2	N levels	(a)	0.0 kgN ha^{-1}
		(b)	124.5 kgN ha^{-1}
2	P levels	(a)	0.0 kgP ha^{-1}
		(b)	100.0 kgP ha^{-1}
2	Basal levels	(a)	No Basal
		(b)	K, Ca, Mg, S Basal at standard rate.

Treatments were replicated three times giving a total of 48 pots, 24 pots being common with the main experiment.

5.2.2. Soils.

Soils were collected on 15 February 1983 from each terrace of Puffers Stream, adjacent to the soil pits and two terraces at the Craigieburn site, Cave Stream (Chapter 1.4). The Craigieburn main terrace (CB4) was sampled as described in Section 8.2 and the youngest terrace at Cave Stream (CB1) was sampled 3m from the bank (Terraces CB4, (= C1 and C4 Tonkin 1980): Grid Reference S66 206027). Surface vegetation was carefully removed and the upper Ah horizon excavated to 10cm for all soils.

Soils were air dried for a week in the glasshouse, passed through a 6mm sieve and 450gm weighed (± 0.2g) into a 10 x 12cm polystyrene pot lined with Whatmans No.6 filter paper. All pots were saturated with deionised water and allowed to drain.

Fertilisers were surface applied in solution by 10 ml pipette ± 0.1ml on 28 – 29 March for the main experiment and on 9 April for supplementary experiments as follows:

Compound (Analar Grade)	Form	Elemental Rate ($kg\ ha^{-1}$)	
Potassium dihydrogen phosphate	KH_2PO_4	K 126.0	P 100.0
Potassium sulphate	K_2SO_4	K 50.0	S 20.5
Magnesium sulphate	$MgSO_4$	Mg 20.8	S 27.4
Calcium chloride	$CaCl_2\ 2H_2O$	Ca 25.4	Cl 44.1
Potassium chloride	KCl	K 135.8	Cl 133.3
Magnesium chloride	$MgCl_2\ 6H_2O$	Mg 50.0	Cl 145.9

Each pot was placed in a 12.5 x 2cm deep tray and regularly bottom watered throughout the experiment with deionised water. Watering frequency increased from weekly to every one and a half days by the termination of the experiment.

5.2.3. Tussocks

Ten Fescue tussocks from Puffers Stream and Craigieburn main surfaces (see Section 8.2) were sampled at the same time as soils. Thirty large tillers with ≥ 3 live leaves were selected per tussock, stripped of dead leaves and sheaths and old roots between 1-3 leaf scars below the base of the outermost living sheath. The stem below the third leaf scar was removed. New roots, just initiated but < 0.1cm were left intact. Tillers were planted in a glasshouse sand bed mist box, maintaining 10 distinct clone lines for each population, on 18 February.

Plants were lifted on 5 March and dead or senescent leaves removed. Tillers with ≥ 3 live leaves and leaf lengths ≥ 20cm were graded on root number and size. Roots were gently blotted dry, tillers weighed ± 0.1g, tiller visible leaf and root number counted and each root length measured (± 1mm). Fifteen plants were oven dried for 24 hours at 70 °C, weighed and retained for nutrient analyses.

The main experiment was potted on 8 March. Clone lines were randomly positioned for each fescue tussock population by random number. The supplementary experiments were planted three days later. Twenty one plants which failed to establish were replanted with spare tillers between 13 - 22 April. All three experiments were mixed and randomised in four blocks with pots 15cm apart. Pots were re-randomised within blocks on 20 June and 26 August. Pots were regularly weeded throughout the experiment.

5.2.4.Harvest

Pots were harvested on 20-21 September 1982. Plants were cut at the sheath base-root junction with a scalpel and sheath bases rinsed free of any adhering soil particles in deionised water. The number of tillers, live and dead, and the number of visible leaves (ignoring the youngest intervaginal leaf, if present but not exposed) were counted. Live tiller and leaf number were defined as follows:

live tiller	: Any tiller with a green leaf, partial or complete, present.
live leaf	: Any leaf with > 50% green tissue.

The longest leaf length was measured from sheath base to tip along a graduated ruler ± 1.0mm. Tops were oven dried for 48hrs at 70 °C, weighed ± 0.1g, ground to pass through a 0.5mm sieve, and stored for nutrient analysis. Roots were gently washed free of soil over a 1mm sieve, oven dried for 48hrs at 70 °C and weighed ± 0.1g.

5.2.5 Statistical Analysis

All data were analysed using GENSTAT (Alvey *et al.* 1983) as specified in Chapter 2.2. Statistical conventions used in this chapter are also described in Chapter 2.2.

5.3 RESULTS

5.3.1 Soil-Phosphorus-Basal Experiment

Soils and phosphorus were the factors responsible for the largest variation in fescue growth. Their main effects and interaction accounted from 46.4% (root DM) to 64.0% (shoot DM) of the total sum of squares in analyses of variance. The effects of basal fertilisers and fescue population were smaller. Treatment effects are summarized for the major growth parameters in Table 5.2.

Table 5.2: Effect of treatment factors on tussock growth (Analysis of variance probability levels: significant values emphasised).

Factor	Tiller No	Leaf No	Shoot DM	Root DM	Total DM
Soil	**<.001**	**<.001**	**<.001**	**<.001**	**<.001**
Basal	.627	.974	.181	.214	.133
Population	.212	.852	.988	.755	.810
Phosphorus	**<.001**	**.001**	**<.001**	**<.001**	**<.001**
Soil x Bas.	.265	.533	.074	.502	.157
Soil x Pop.	.076	.163	.094	.063	.059
Bas. x Pop.	.170	.087	**.026**	.121	**.043**
Soil x P	.140	**.010**	**.001**	**.022**	**.001**
Bas. x P	.511	.583	.346	.308	.260
Pop. x P	.260	.532	.854	.189	.434
Soil x Bas. x Pop	.682	.140	**.034**	.178	.070
Soil x Bas. x P	.156	.380	.395	.535	.488
Soil x Pop. x P	.581	.894	.750	.726	.770
Bas. x Pop. x P	.354	.894	.718	.789	.758

It is unclear whether the soil x basal x population interaction is an experimental artifact or is biologically significant. The significance of the interaction (Table 5.2) depended on a single plant. Inclusion of this ramet, with the lowest DM in the entire experiment (only 0.03 g) altered the significance levels for shoot DM to $p < 0.227$ and for total DM to $p < 0.241$. This indicates the increasing sensitivity of the factorial analysis of variance to outliers as the interaction level increases and replication within each level decreases.

(a) The effect of P and soil

Phosphorus application significantly increased tiller and leaf production with significant differences between soils ($p < .001$; Tables 5.3, 5.4) and a significant soil x P interaction for leaf production ($p < .010$).

Table 5.3: Response of tiller number per plant to applied P on Craigieburn and Puffers Stream Soils.

	APPLIED PHOSPHORUS (kg P ha^{-1})		
SOIL	0	100	MEAN
CB 1	8.5	15.8	**12.1**
CB 4	13.6	26.1	**19.9**
T 1	10.0	11.3	**10.6**
T 2	21.2	29.6	**25.4**
T 3	17.7	22.3	**20.0**
T 4	21.9	26.9	**24.4**
T 5	9.9	21.9	**15.9**
MEAN	**14.5**	**22.0**	

SEM Soil = 1.5; P = 0.8; Soil x P = 2.2.

Table 5.4: Leaf production on Craigieburn and Puffers Stream Soils with applied phosphorus (Leaf number per plant).

	APPLIED PHOSPHORUS (kg. P ha^{-1})		
SOIL	0	100	MEAN
CB 1	28.7	52.0	**40.3**
CB 4	45.1	95.0	**70.0**
T 1	35.8	37.8	**36.8**
T 2	67.0	85.8	**76.4**
T 3	54.3	75.8	**65.1**
T 4	72.2	94.1	**83.1**
T 5	34.4	77.7	**56.1**
MEAN	**47.5**	**74.1**	

SEM Soil = 4.8; P = 0.5; Soil x P = 0.7.

The number of leaves produced per tiller was remarkably constant across P and soil treatments (Fig. 5.1):

$$\text{Leaf No} = \underset{(4.00)}{1.58} + \underset{(0.20)}{3.24}\ \text{Tiller Number} \qquad r = .954\ ***$$

where ( ) is the standard error of the parameter.

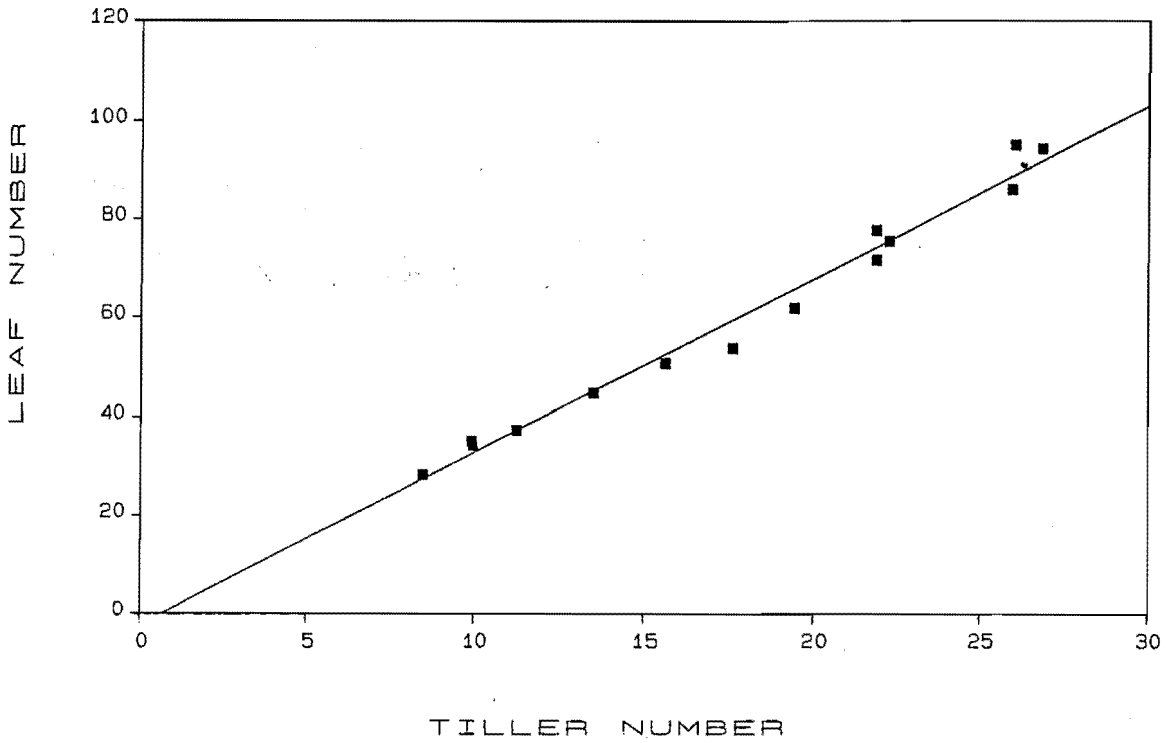


Figure 5.1 : The relationship between number of leaves and tillers in fescue tussock

The highly significant soil x P interaction with total DM ($p < .001$; Fig. 5.2) and shoot production ($p < .010$; Fig. 5.3) was due to the greater P response on CB4 and T5 relative to other soils. The interaction was also significant for root production ($p < .022$) but only CB4 showed a large P response (Fig. 5.4).

The dramatic increase in plant DM with applied P is self evident (Figs. 5.2 and 5.3). The main effect of soils is summarized in Table 5.5.

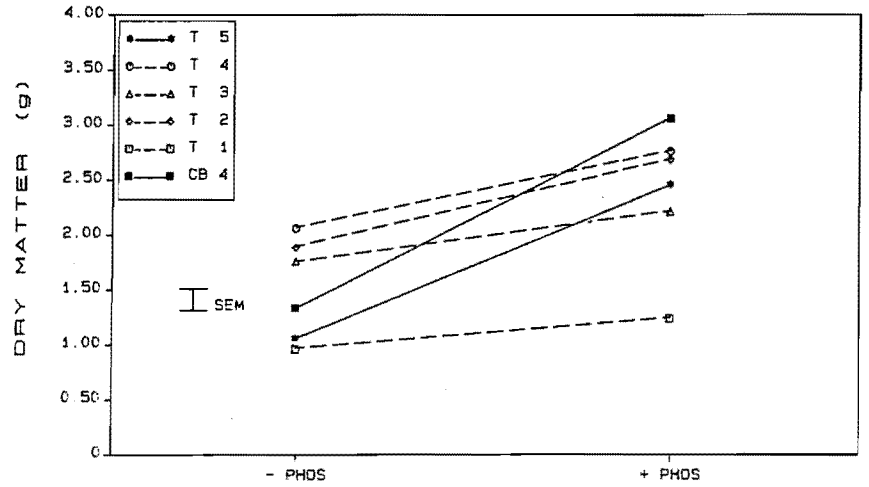


Figure 5.2 : The effect of P on fescue tussock Total DM production on soils T1 - CB4

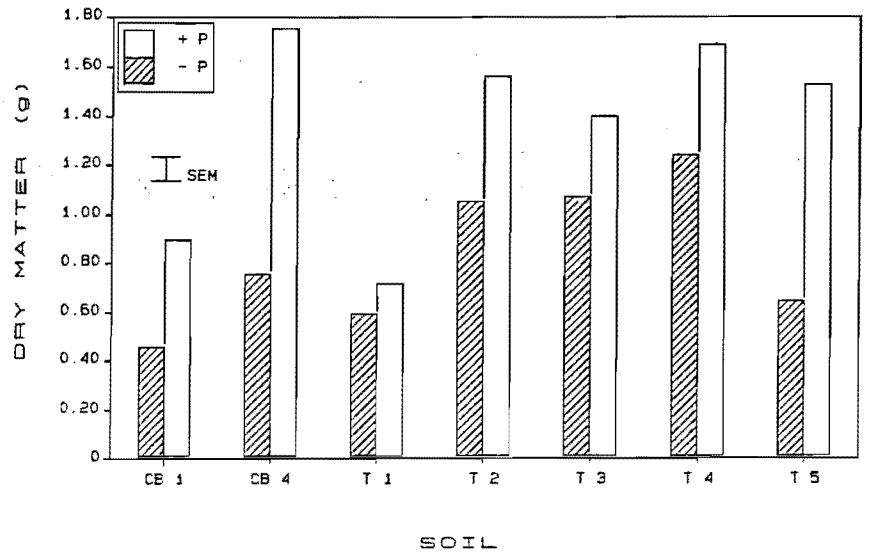


Figure 5.3 : The effect of P on fescue tussock shoot DM production on soils T1 - CB4

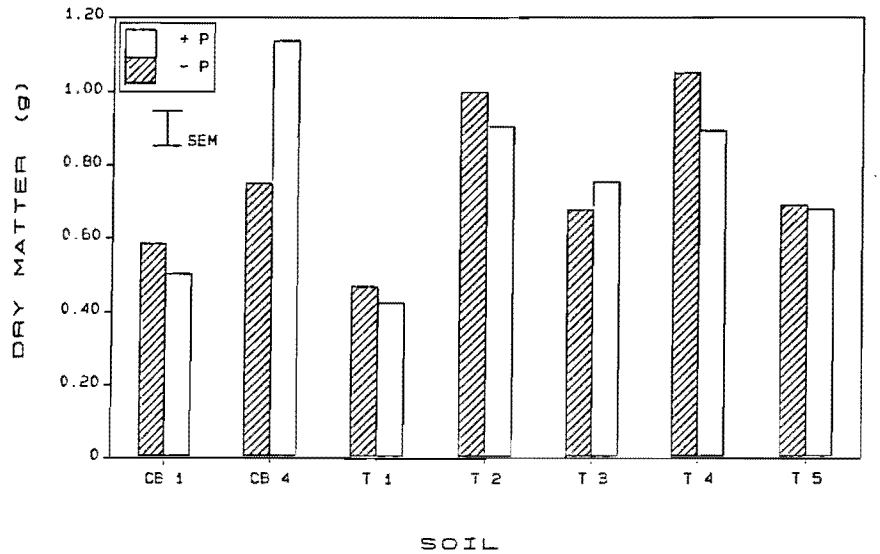


Figure 5.4 : The effect of P on fescue tussock root DM production on soils T1 - CB4

Table 5.5: Main effect of soil on fescue DM production averaged across P and basal treatments (g DM).

	Soil								
Parameter	CB1	CB4	T1	T2	T3	T4	T5	SEM	p
Shoot DM	.68	1.26	.66	1.34	1.23	1.46	1.08	.07	<.001
Root DM	.58	.95	.45	.97	.75	.97	.68	.07	.001
S:R Ratio	1.44	1.40	1.67	1.47	1.90	1.65	1.71	.14	.199
TOTAL DM	**1.23**	**2.21**	**1.11**	**2.31**	**2.00**	**2.43**	**4.77**	**.12**	**<.001**

(b) The effect of fescue tussock population

Tussocks from the Craigieburn and Puffers Stream populations only differed slightly in their response to P but differed in response to soils and differed significantly with addition of basal fertilisers (Table 5.2). Root, shoot and total plant DM of the Craigieburn population showed no response to basal whereas there were significant increases for shoot ($p < .026$) and total DM ($p < .043$) with the Puffers Stream population (Fig. 5.5).

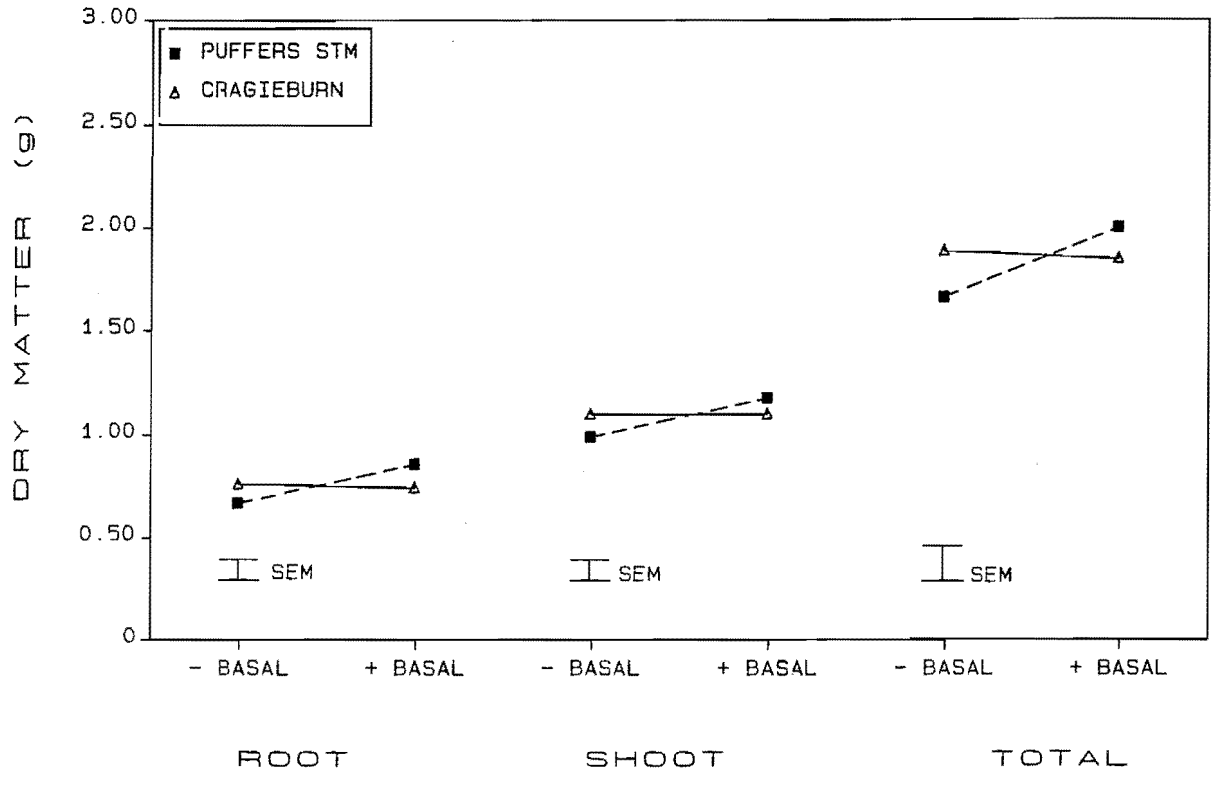


Figure 5.5 : The effect of basal fertiliser on fescue tussock from Craigieburn and Puffers Stream populations

The interaction between soil and fescue population ($p < .059$) is shown for total plant DM in Table 5.6. The highest yield of the Craigieburn population occurred on its native soil CB4 followed by T4. Conversely the highest yield of the Puffers Stream population occurred on T2, slightly higher than on its original soil T4 but much greater than on the Craigieburn soil CB4.

Table 5.6: Total plant DM production on CB1, CB4 and T1-T5 by fescue tussocks from the Craigieburn and Puffers Stream populations (g DM).

Soil	Population	
	Craigieburn	Puffers Stream
CB 1	1.14	1.32
CB 4	2.55	1.88
T 1	1.11	1.12
T 2	2.10	2.51
T 3	2.14	1.86
T 4	2.42	2.45
T 5	1.69	1.84
MEAN	**1.88**	**1.86**

SEM = 0.17

Correlation of each fescue population with untreated topsoil chemical variables differed (Table 5.7). While CEC and C were positively correlated with both populations, tussocks from Craigieburn were strongly correlated with P retention, N, oxalate-extractable aluminium and iron in contrast to the significant correlations with P fractions in the Puffers Stream tussocks. Correlation using the individual P and basal treatments on the 7 soils were essentially similar to the main effect analysis (Table 5.7) and are not presented.

Table 5.7: Correlation of Craigieburn and Puffers Stream fescue DM with soil chemical parameters (correlation coefficient r and probability level; significant values emphasised).

	SOIL PARAMETER									
POPULATION	Ptot	Porg	CEC	C	Al_o	Fe_o	K	BS_c	Pret	N
PUFFERS STM.	.795 (.032)	.763 (.046)	.891 (.007)	.806 (.028)	.715 (.071)	.520 (.023)	.717 (.070)	-.660 (.106)	.400 (.073)	.610 (.146)
CRAIGIEBURN	.582 (.170)	.600 (.155)	.917 (.004)	.890 (.007)	.909 (.004)	.861 (.015)	.851 (.014)	-.786 (.036)	.795 (.033)	.801 (.030)

(c) Correlation of tussock DM and soil chemistry

Soil chemical variables most highly correlated with fescue DM for each of the main treatments, averaged across the two fescue populations, are listed in Table 5.8. Soil data are listed in Table 8.4 and variables described in Appendix 2.2.

Table 5.8: Correlation of Fescue DM production with soil chemical variables and differential fertiliser amendment (Correlation coefficient; (probability level); significant values emphasized).

	SOIL CHEMICAL PARAMETERS								
TREATMENT	CEC	C	Fe_p	Ptot	Porg	Al_o	K	N	Al_p
SOIL	.898 (.006)	.827 (.002)	.802 (.030)	.791 (.034)	.776 (.040)	.779 (.039)	.751 (.052)		
BASAL	.944 (.001)	.933 (.002)	.826 (.022)	.886 (.008)	.871 (.016)	.841 (.012)	.821 (.024)	.832 (.023)	.816 (.025)
PHOSPHORUS	.611 (.145)	.568 (.183)	.433 (.352)	.338 (.458)	.301 (.512)	.591 (.162)	.426 (.340)		.551 (.120)
BASAL + PHOSPHORUS	.882 (.009)	.816 (.020)	.646 (.117)	.578 (.174)	.602 (.153)	.798 (.032)	.854 (.015)	.729 (.063)	.736 (.059)

The soil variables themselves were highly auto-correlated. Carbon was highly correlated with CEC ($r = .970$; $p < .0003$), K ($r = .898$; $p < .006$), pyrophosphate extractable aluminium ($r = .846$; $p < .016$) and iron $r = .716$; $p > .070$) as well as organic P ($r = .783$; $p < .037$). Total P, in turn, was closely correlated with organic P ($r = .984$; $p < .0001$).

Comparing glasshouse results with those from the field, there was poor correlation between shoot DM production from the field transplant experiment (Chapter 4) and from untreated soils in this pot experiment ($r = -0.260$; $p < .673$). The effect of pot trial soil preparation on production, relative to intact soils, is investigated further in Chapter 7.

5.3.2 Basal Fertiliser Rate

Basal fertilisers strongly influenced shoot and root production by interaction with P (Fig. 5.6). The interaction was similar for roots and shoots but near significance only for roots ($p < .057$) and total plant DM ($p < .055$). Root:shoot ratios did not differ significantly with any treatment.

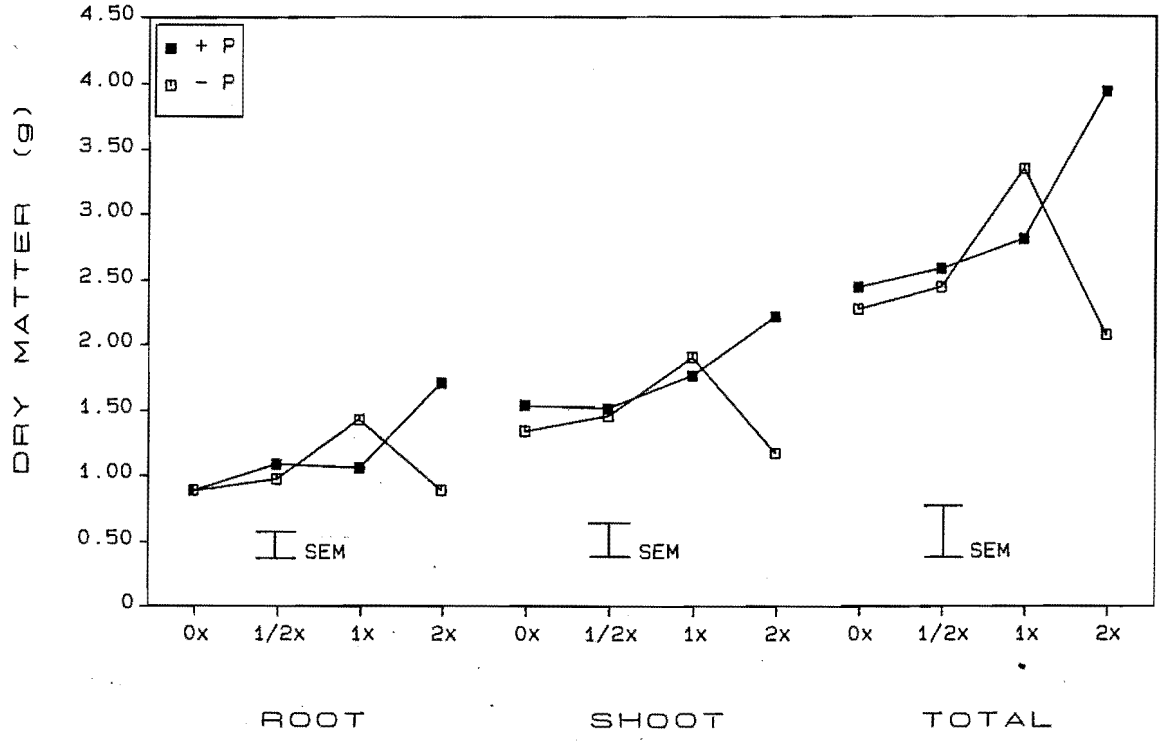


Figure 5.6 : The effect of basal fertiliser rate on fescue tussock DM production

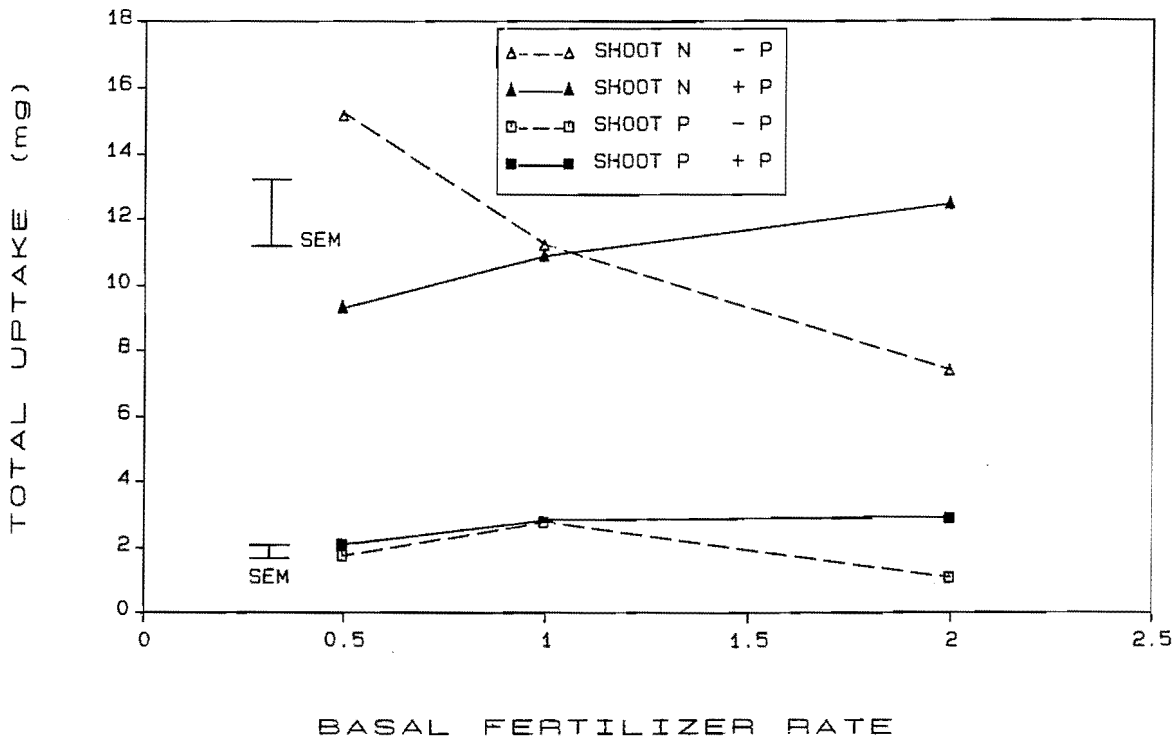


Figure 5.7 : The effect of basal fertiliser rate on fescue tussock shoot N and P concentration

Phosphorus concentrations in live shoots increased from 1.49 to 2.01 mg P g^{-1} DM from half to the standard basal rate, then declined to 1.44 mg Pg^{-1} DM at twice the standard rate ($p < .001$). As expected, tissue P concentration were significantly higher with applied P (1.85 vs 1.44 mg P g^{-1} DM; $p < .002$). The P by basal interaction was not significant ($p < .896$).

Shoot N concentration decreased slightly, but not significantly, as basal rate increased (Table 5.9). Phosphorus application did not alter significantly tissue N concentration ($p < .173$) nor was the P by basal interaction significant ($p < .187$, Table 5.9).

Phosphorus application, as expected, significantly increased shoot P concentration, the effect depending on the rate of basal fertiliser (Table 5.10). Basal fertiliser did not interact significantly with other treatments. Total P uptake was greater with applied P ($p < .055$) with little difference between basal treatments ($p < .119$, Fig. 5.7). Nitrogen uptake increased with increasing basal rate when P was present but sharply declined without P ($p < .060$, Fig. 5.7).

Table 5.9: Live shoot N concentration with varying rates of basal and P fertiliser (mg N g^{-1} DM).

	Applied P (kg. P ha^{-1})		
Basal Rate	0	100	MEAN
1/2x	11.45	7.90	9.67
1x	7.44	8.24	7.84
2x	8.07	6.89	7.48
MEAN	8.99	7.68	

SEM Basal = 0.78; P = 0.64; Basal x P = 1.107

Table 5.10: Live shoot P concentration with varying rates of basal and P fertiliser. (mg P g^{-1} DM).

Basal Rate	Applied P (kg. P ha^{-1}) 0	100	MEAN
1/2x	1.32	1.67	1.49
1x	1.78	2.24	2.01
2x	1.23	1.64	1.44
MEAN	1.44	1.85	

SEM Basal = 0.09; P = 0.07; Basal x P = 0.13.

5.3.3 Basal Fertiliser Composition

Phosphorus, soil and basal fertilisers all significantly affected tussock growth with P the major factor, accounting for over half the variability in the analysis of variance (Table 5.11). Phosphorus interacted significantly with soil in root, shoot and total DM production and also with basal fertiliser for total DM production. Shoot DM also varied significantly depending on basal fertiliser and soils (Table 5.11).

The response to P was clearly greater on the Craigieburn soil compared with Puffers Stream, causing the soil x P interaction (Fig. 5.8). Similarly, the greater growth on the Craigieburn soil when basal cations were supplied as chloride, rather than sulphate, salts was responsible for the soil x basal interaction (Fig. 5.9). Basal chlorides depressed root and shoot production in the absence of P but not when it was present, causing the striking basal x P interaction (Fig. 5.10).

Table 5.11: Effect of basal fertiliser, soil and phosphorus on fescue DM. (ANOVA % Sum Squares; probability levels; significant values emphasized).

Treatment	Shoot DM ss%	p	Root DM ss%	p	Total DM ss%	p
Soil	3.0	.058	8.2	.020	5.8	.009
Basal	10.0	.005	8.0	.067	9.8	.004
P	53.2	.001	45.9	.001	56.4	.001
Soil x Basal	6.1	.031	.4	.857	2.0	.270
Soil x P	7.5	.005	7.8	.024	8.6	.002
Basal x P	5.0	.054	4.6	.201	5.3	.039
Soil xBas. xP	2.7	.189	3.0	.341	3.1	.136

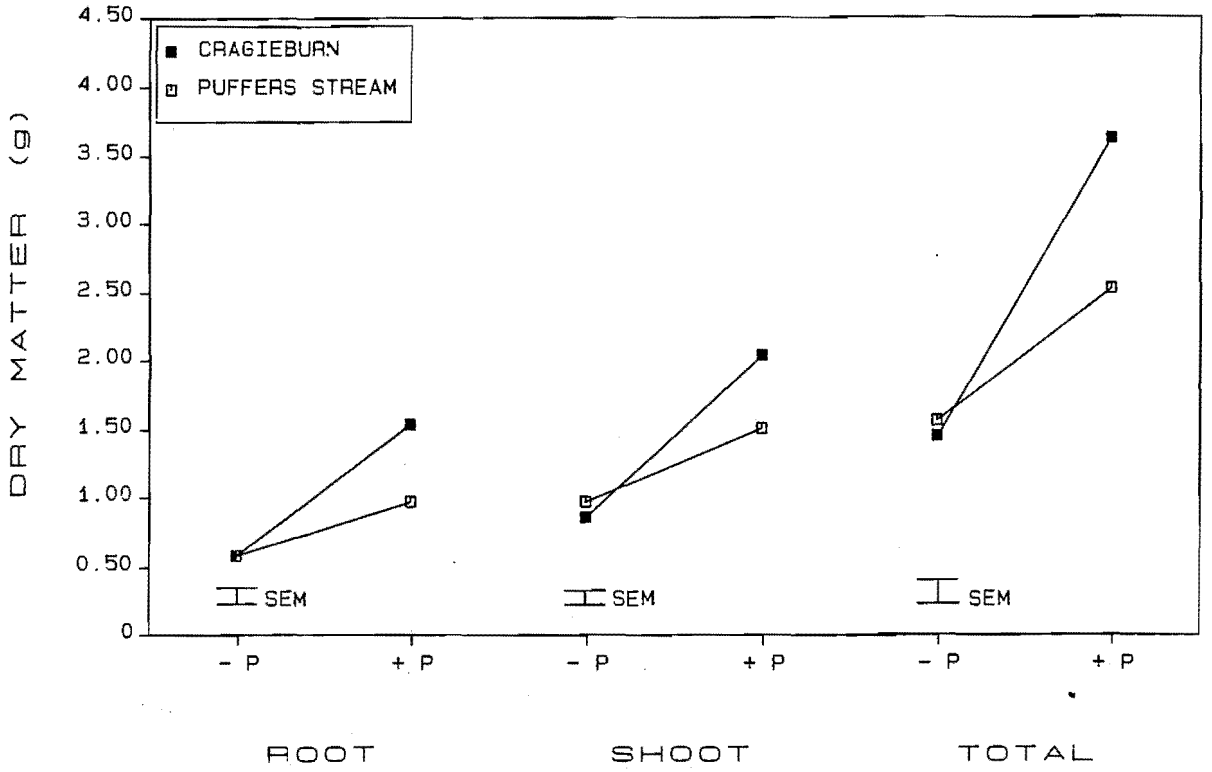


Figure 5.8 : The P response of fescue tussock on Craigieburn and Puffers Stream soils

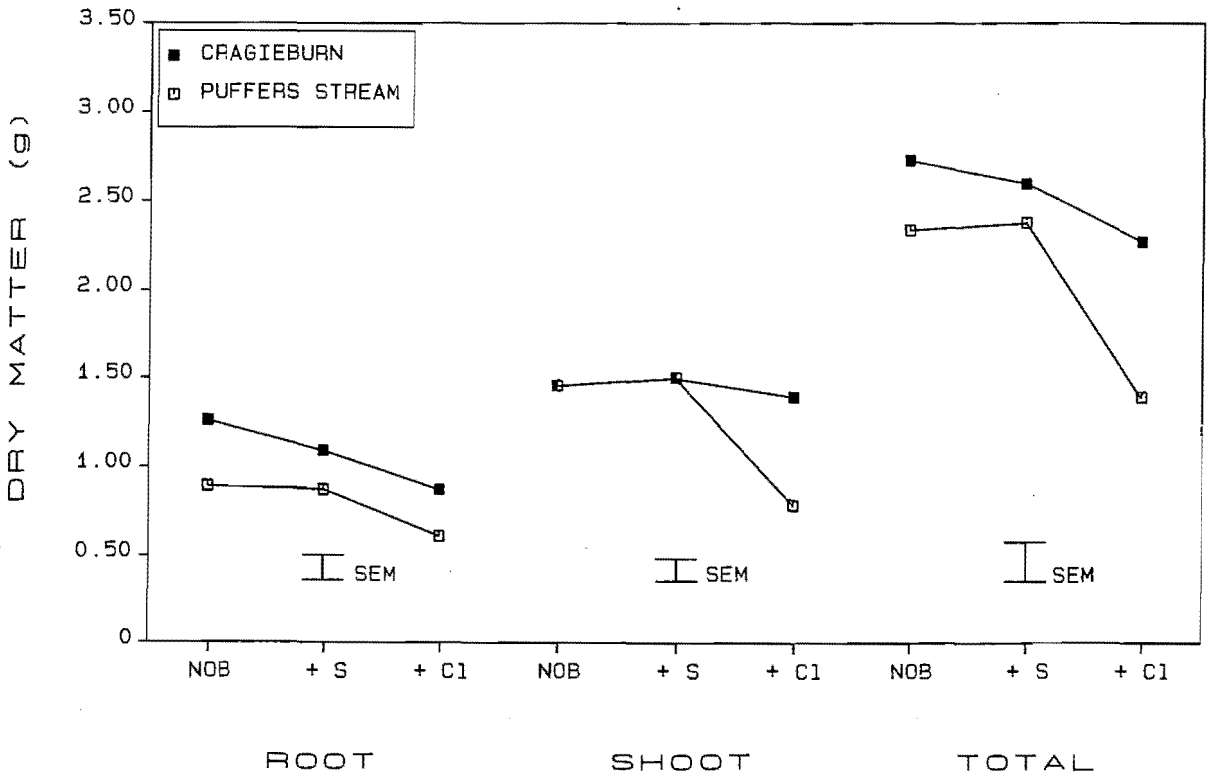


Figure 5.9 : The effect of basal fertiliser rate on fescue tussock DM on Puffers Stream and Craigieburn soils.

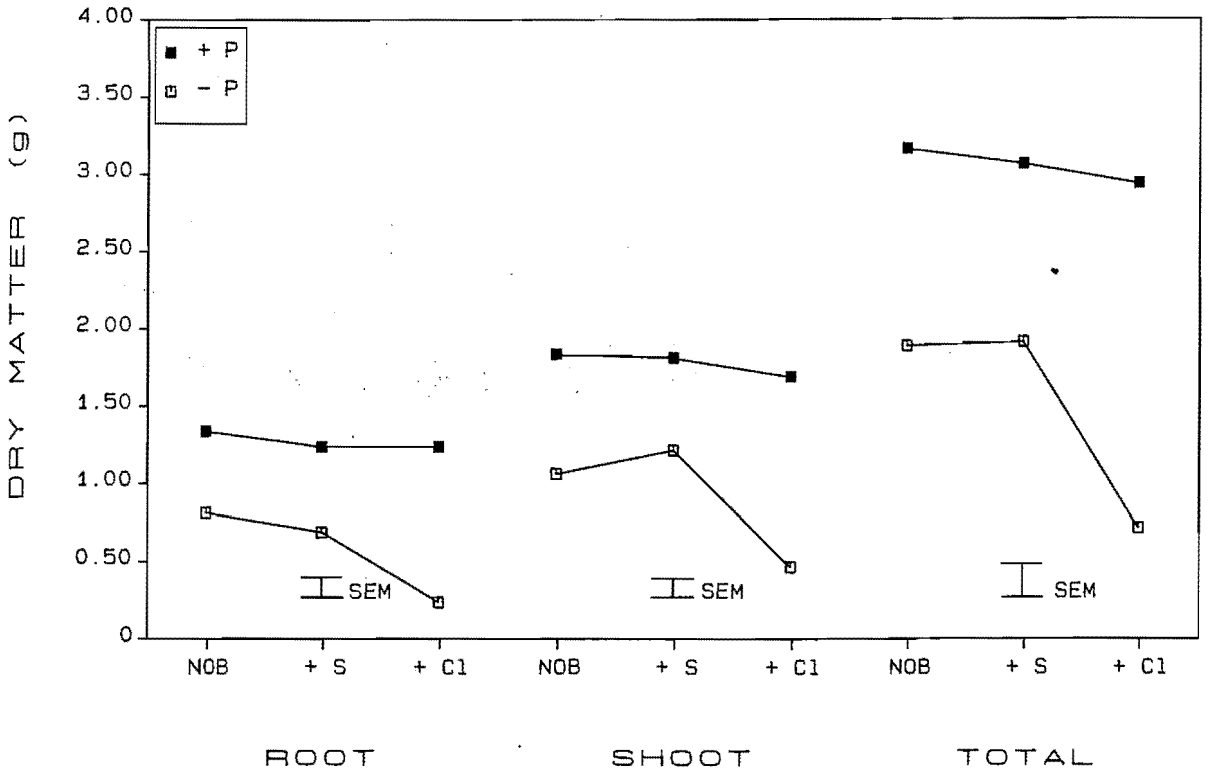


Figure 5.10 : The effect of basal fertiliser composition and applied P on fescue tussock DM production

5.3.4 Nitrogen Fertiliser

Nitrogen and particularly phosphorus strongly influenced fescue growth with soil and basal fertilisers having a smaller, though significant, effect through interaction with N and P (Table 5.12).

Table 5.12: Effect of soil N, P, and basal fertiliser on tussock growth.
(ANOVA % sum of squares; significance level, significant values emphasized.)

Factor	Root DM %ss	p	Shoot DM %ss	p	Total DM %ss	p
Soil	1.2	.282	0.0	.693	0.0	.782
Basal	0.0	.841	0.5	.221	0.1	.572
P	46.4	**<.001**	42.3	**<.001**	47.8	**<.001**
N	2.9	.098	13.1	**<.001**	9.5	**<.001**
Soil x Basal	0.3	.585	0.0	.725	0.0	.880
Soil x P	0.0	.882	0.0	.900	0.0	.912
Basal x P	0.0	.965	5.4	**<.001**	2.6	**.020**
Soil x N	0.8	.385	0.0	.862	0.1	.710
Basal x N	0.7	.396	1.4	**.049**	0.2	.464
N x P	10.5	**.003**	16.9	**<.001**	16.3	**<.001**
Soil x Bas x P	0.0	.958	0.3	.365	0.1	.600
Soil x Bas x N	1.0	.320	0.2	.477	0.0	.918
Bas. x N x P	4.9	**.035**	2.3	**.011**	3.3	**.009**
Soil x N x P	0.1	.783	3.3	**.003**	1.7	.054

The basal x N x P interaction was due to two contrasting effects. With P, the addition of N gave a large increase in yield but when basal was also present the increase was smaller (Fig. 5.11). Conversely, without P, the addition of N depressed yield whereas N plus basal had no effect (Fig. 5.11).

The second three factor interaction, between soil x N x P, was caused by the greater response on Puffers Stream soil to N plus P compared with Craigieburn and the depression in yield on Puffers Stream soils with N in the absence of P compared with the slight increase in Craigieburn Soil (Fig. 5.12).

The strong second order interaction between N and P is easily seen in Figs. 5.11 and 5.12. Addition of P alone, averaged over both soils, increased DM yield 1.7 times whereas addition of N alone had little effect. However the addition of N and P together gave a three fold increase in DM production. In contrast, the joint application of P and basal (Fig. 5.11) resulted in lower production compared with only P application. Addition of basal alone only slightly increased shoot DM yield.

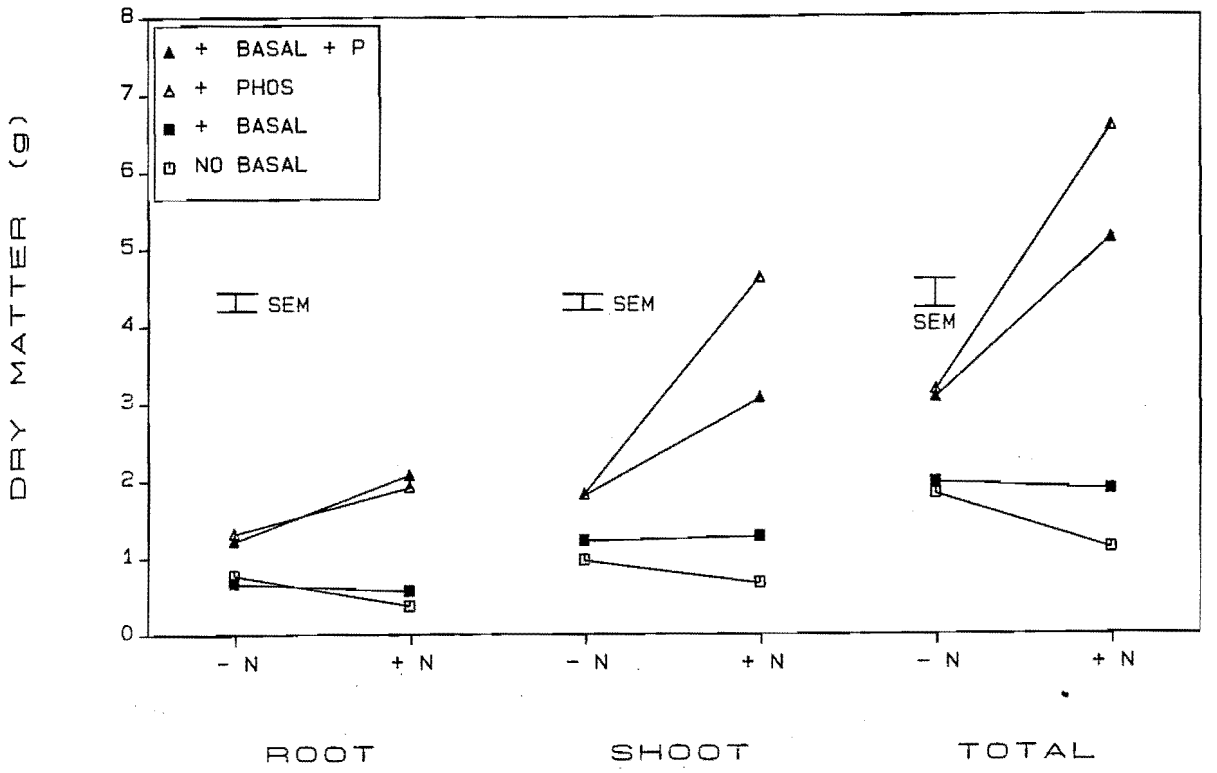


Figure 5.11 : The interaction of N, P, and Basal fertilisers and fescue tussock DM

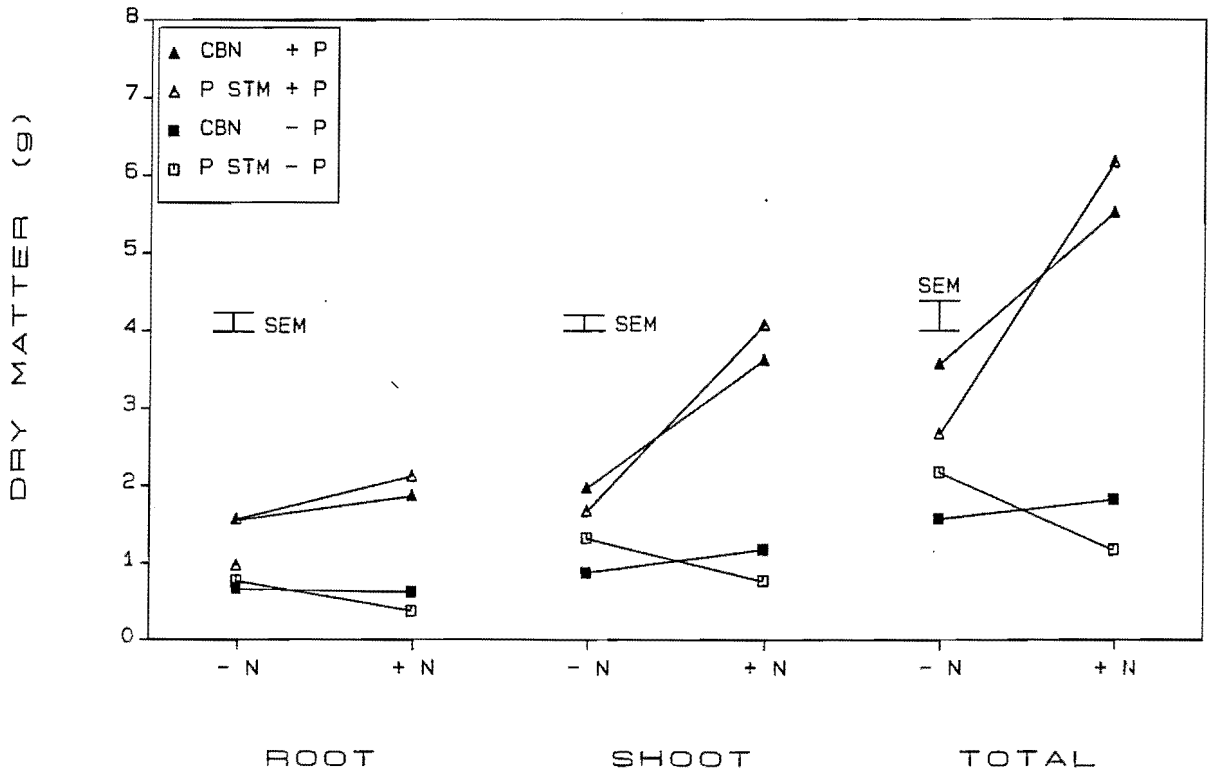


Figure 5.12 : The interaction of soil N, and P fertilisers and fescue tussock DM

5.4 DISCUSSION

5.4.1 Soil-Phosphorus-Basal Experiment

The constant ratio of leaves per tiller across a wide range of edaphic conditions (Fig. 5.1) shows growth in fescue tussock is determined, by unit shoot production rather than by variation in number of shoot components. Unfortunately, though variation in shoot:root biomass partitioning occurred (Table 5.5) the replication and sensitivity of this experiment was insufficient to confidently assess the true biological significance of the ratios.

Mineral nutrition, particularly P nutrition, had a large influence on fescue growth (Table 5.2, Figs. 5.2, 5.3, 5.4). Examining the soil x P interaction it is interesting the greatest P response, responsible for the interaction, occurred in CB4 and T5, the oldest soils in both sequences (Fig. 5.2). This pairing is consistent with their pedological development. Terrace 5 is probably older than CB4 but the higher rainfall and greater leaching at Craigieburn would result in a faster weathering rate relative to Puffers Stream (see Webb *et al.* 1986)

The large P response in T5 and CB4, relative to other soils, may be due to P amelioration of Al toxicity (Bollard 1983). Exchangeable Al levels increased markedly with pedogenesis in similar high country yellow brown earth soils formed in greywacke derived loess (Webb *et al.* 1986). This explanation is consistent with the observed P response and the strong negative correlation with exchangeable Al in the field transplants (Chapter 4). It also explains the greater P response on subsoils (Dunbar 1974), where exchangeable Al levels are high compared with topsoils (Davis 1983a). Thus the surprising absence of a significant correlation with exchangeable Al using 0-10 cm topsoil data (Table 5.8) may be due to sampling. Topsoil exchangeable Al values in CB3, formed in the same loess mantle as CB4, were 2.3 milliequivalents percent (me%) compared with the 1.0 me% reported for CB4 (Tonkin 1981) although the two profiles were within 50m. Similarly the 0-10 cm exchangeable Al levels in T5 (1.7 me%) may be lower than the actual levels present in the potsoil, considering the very high (5.4 me%) levels present in the underlying 10 cm. It is quite possible some of this material extended closer to the surface in the soil sampled through deflation or local variation.

The low DM production on T1 and CB1, the youngest soils in both sequences, either with or without P (Fig. 5.2) is hard to explain but suggests some factor(s) other than P are responsible. Nitrogen is a possibility since it is the only macronutrient, discounting sulphur and potassium (Section 5.2), occurring at low levels on these terraces relative to other soils. Furthermore, N is significantly correlated with fescue production in some instances (Table 5.8). If N deficiency is responsible for growth limitation then the high shoot N concentrations in the field (Chapter 3) and transplanted (Chapter 4) tussocks must derive either from greater field availability or from sources deeper in the profile.

Nevertheless the low production on T1 and CB1 is consistant with mineralogical analyses from the adjacent Camp Stream alluvium and alluvial soils (Camp Stream Series). Samples had over six times the amount of amorphous minerals but only half as much feldspar as unweathered greywacke fragments from the parent rock and thus were less fertile than expected (Furkert *et al.* 1975). It seems reasonable from the similarity of the parent rock (Chapter 1.4) to infer a similar composition of the alluvium in Cave and Puffers Streams.

The fundamental importance of the soil organic regime in fescue mineral nutrition is shown by the close correlation of DM with soil factors associated with organic matter and highly autocorrelated with carbon (Table 5.8). Organic P, and also N, considering the strong N x P interaction (Section 5.3.4), are probably the key elements involved. This is suggested by only a minor change in correlation coefficients with the addition of basal fertilisers compared with the removal of all significant correlation with addition of P (Table 5.8). Organic N is probably responsible for the reappearance of the significant correlation with C, K and CEC (Table 5.8) with the addition of basal fertilisers plus P, as the other macro-nutrients were all present. The addition of basal anions, particularly chloride, through antagonism may reduce N availability (Section 5.3.2), thus making it a limiting factor and hence closely correlated with yield.

The different response by the fescue populations to basal fertiliser (Fig.5.5), parent soil (Table 5.6) and soil chemistry (Table 5.7) is clear evidence for ecotypic differentiation within the species. If phenotypic plasticisity within the same genotype was responsible (Bradshaw 1965, 1973, Grime *et al.* 1986) as Greer (1979) has shown in *Chionochloa rigida* and Fisher (1960) in *Rannunculus hirtus*, then both populations would exhibit the same response to edaphic factors.

It is well established that a frequent plant response to environmental heterogeneity is the development of locally distinct ecotypes (Bradshaw 1972). Greater precipitation and consequently leaching at Craigieburn (Chapter 1) has resulted in a slightly less fertile environment relative to Puffers Stream. In the upper T4 topsoil (0-10 cm) at Puffers Stream, base saturation and P, Ca, Mg, K and Na levels range from 2.3 to 1.2 times greater than those on CB4 at Craigieburn (Table 8.4).

Festuca novae-zelandiae is an outcrossing species with low self-fertility (Connor & Cook 1955, Connor 1960b). It is a lowland plant considered originally '... *adapted to riverbeds and recent landforms*' (Connor 1968) while the closely related *F. mathewsii* was restricted to sub-alpine and alpine grasslands (Connor 1961, 1964, 1968). The period of fescue tussock grassland following forest destruction in the eastern South Island ca. 600 yrs B.P., as discussed in Chapter 1.5, Connor (1961, 1964) and O'Connor (1986), is more than adequate for ecotypic differentiation to develop between fescue populations (see Bradshaw 1965, 1972, Harper 1977). Lambrechtsen 1968 provided evidence of ecotypic adaptive variation in *Anthoxantum odorarum* in similar environments during only european occupation. It seems reasonable therefore to infer geographic separation proved an effective barrier to gene exchange between the two study sites, thus allowing genotypic adaptation.

The greater response of the Puffers Stream population to basal fertilisers, its high correlation with soil P fractions and lower DM production on CB4 relative to the Craigieburn plants are consistent with the differences in soil leaching regime. The Puffers Stream population evidently retains the ability, from the original fescue tussock niche in fertile alluvial sites, to respond to an improvement in nutrient supply by increased growth. This is characteristic of high-fertility adapted plants, giving competitive advantage where often the primary limitations to growth are above ground or water supply (Chapin 1980). The strategy of rapid growth and resource acquisition is of little advantage, or is even disadvantageous in less fertile environments (Chapin 1980).

Conversely, plants adapted to resource-poor sites have slower growth rates and may sequester nutrients taken up during flushes, with no increase in production, as a buffer against future nutrient limitation. Thus the absence of a response to basal in the Craigieburn population appears more characteristic of the type of plant adapted to highly leached and/or infertile habitats (Grime 1977, Chapin 1980, Schultz & Chapin 1987).

The significant correlation of the Puffers Stream population with soil P compared with the Craigieburn population (Table 5.7) may indicate a lower P requirement in the Craigieburn plants and hence less responsiveness to variation in soil P. The form of the population by P interaction was similar to the population by basal interaction though differences in the population by P interaction were not large enough to be significant (Table 5.2). Without P Craigieburn plants outyielded Puffers Stream, with P the reverse occurred, consistant with the argument for edaphic adaption.

Plant nutrition is rarely a single factor system, it is usually multi-factorial with many possible interactions and plant responses (Schultz & Chapin 1987). The superior growth of the Craigieburn population on its own soil, CB4, relative to Puffers Stream and the similar performance of both populations on Puffers Stream T4 may possibly indicate another factor. Craigieburn plants may be tolerant to factor(s) which limit tussocks from Puffers Stream. If the proposed explanation for the soil by P interaction is correct then differential tolerance to exchangeable Al may also be involved. This may also be linked with interference in P nutrition (see Bollard 1983). Furthermore interaction with mycorrhizae cannot be discounted (see Hall & Armstrong 1979, Hall 1980).

There are relatively few demonstrations of ecotypic differentiation in the New Zealand flora (Connor 1985). A high altitude form of *Festuca novae-zelandiae* was recognised by Connor (1960a, 1968) which was subsequently shown to have its highest relative growth rate at a lower temperature than the lowland form (Scott, 1970).

Ogden (1974) established that two ecotypes occur in *Selliera radicans*. Lee *et al.* (1983) investigated 15 species for ultramafic tolerance finding evidence for ecotypic differentiation in *Luzula crinita* var *petriana, Poa colensoi, Neopaxia australasica, Cotula pyrethrifolia,* and the naturalized grasses *Agrostis tenuis, Anthoxanthum odoratum* and *Lolium perenne*. Lyon *et al.* (1971) claim ultramafic ecotypes for *Leptospermum scoparium, Hebe odora* and *cassinia vauvilliersii*. Wardle *et al.* 1973, Cook *et al.* 1980 and Yin *et al.* 1984 present convincing data for ecotypic variation in *L. scoparium* with response to altitude

environmental variability, soil infertility and drainage. Wardle (1969) also reported lowland and subalpine ecotypes of *Phyllocladus alpinus*. A prostrate geothermal form of *Kunzia ericoides* retained its habit in cultivation, (Given 1980). *Chionochloa*, a genus with widespread intraspecific variability (Connor 1985), almost certainly has more ecotypes than already demonstrated in *C. rigida* and *C. flavescens* (Mark 1965, Greer 1979, Connor 1985).

5.4.2 Basal Rate

The basal rate experiment established that the rate of basal fertilisers used in the main experiment (x 1) was not detrimental to tussock growth. It also showed the effect of increased Ca, Mg, K and S supply at the standard rate were minor, causing only a small and non-significant increase compared with untreated soil (Fig. 5.6).

The dramatic depression in DM production at twice the standard basal rate was probably due to anion antagonism. This is shown firstly by amelioration when P was added (Fig. 5.6) and secondly by the decrease in N and P shoot tissue concentration and uptake as basal rate increased (Fig. 5.7). Antagonism between Cl^- and NO_3^- is well established (Robson & Pittman 1983) and the high levels of applied sulphate (98.5 kg S ha^{-1}) and chloride (88.2 kg Cl^- ha^{-1}) reduced N and P uptake and probably caused induced P and N deficiencies. In sharp contrast, the large DM increase when doubling basal rate with P (Fig. 5.6) demonstrates that P addition removed the depression and also that secondary limitation of either base cations or sulphur occurs on unamended soils when P supply is adequate.

5.4.3 Basal Fertiliser Composition

Basal supplied as sulphate salts did not significantly increase fescue tussock DM production on either Craigieburn (CB4) or Puffers Stream (T4) soils whereas chloride salts significantly reduced production on both soils (Fig. 5.9). Similarly without applied P, sulphate salts caused little change but chloride salts significantly depressed yield (Fig. 5.10; Table 5.11). Anion antagonism, as discussed in the previous section, is the most likley explanation for these results.

Without P amendment the Craigieburn soil was more P deficient than the Puffers Stream soil, as shown by the lower fescue shoot production and the higher proportional allocation of resources to root production (Fig. 5.8). With P, the response was greater with CB4 than T4, causing the significant soil x P interactions (Table 5.11). The greater P response on CB4 is probsbly due to both soil structure and chemistry. When air-dried, N levels in CB4 appear higher than in T4 (Chapter 7). As N strongly interacts with P increasing fescue growth (Section 5.3.4) the interaction would probably be greater in CB4 and this could easily account for the higher growth. Furthermore the lower bulk density of

CB4 (Chapter 7) would provide a better physical growth medium through easier root penetration, greater mass water flow and gas diffusion (Russell 1973).

Shoot DM was also greater on the Craigieburn soil relative to Puffers Stream when basal chlorides were applied (Fig. 5.9) causing the significant soil x basal interaction (Table 5.11). As with the basal rate experiment, P addition ameliorated chloride depression, (Fig. 5.10) causing a significant P x basal interaction in both shoot and total DM (Table 5.11). The lower chloride depression in the Craigieburn soil is consistent with the postulated higher N levels. Evidently sufficient N was available, even with applied Cl^-, for adequate growth whereas the reverse was true for T4.

5.4.4 The effect of Nitrogen

The P response and strong N x P interaction (Fig 5.11; Table 5.12) confirm earlier results with a Tekoa steepland topsoil from Bealey (Morrison 1958) and with an eroded Kaikouran subsoil from Porter's Pass (Dunbar 1974). The increase in shoot production with applied N and P was very similar on the two topsoils, 3.4 fold (this experiment) against 3.6 fold (Bealey), but were much lower than the 11.0 fold increase on the Porters Pass subsoil. Dunbar also reported a greater increase in tiller number (5.5 times) than in this study (2.9 times). Reasons for this have already been discussed in section 5.4.1.

Without P, neither N or composite basal (Mg, Ca, K and S), either alone or combined, significantly increased DM production above untreated soil (Fig. 5.11). Similarly, Dunbar (1974) reported extremely poor growth response to K, Mg and N in the absence of P and Morrison (1958) found N, K and S treatments without P had little effect.

In this experiment addition of basal to N plus P depressed yield relative to N plus P alone (Figs. 5.11, 5.13). This differs from Morrison's (1958) results where addition of either K or K plus S to N plus P continued to increase yields. Morrison applied 90 kg N ha^{-1} and 216 kg P ha^{-1} compared with 124.5 kg N ha^{-1} and 100.0 kg P ha^{-1} in this experiment and he did not include magnesium, but even so it is hard to account for the differences.

The depression in production on T4 relative to CB4 when N was applied without P and the proportionately greater response when P was added with N (Fig. 5.12), causing the significant soil x N x P interaction (Table 5.12), suggests N addition may have interfered with P, or other anion, nutrition on the Puffers Stream soil. The exact mechanism is unclear.

5.5 CONCLUSION

Fescue tussock has a determinate vegetative growth pattern, varying shoot production (tiller number) rather than the number of shoot components (leaves per shoot).

Phosphorus caused the greatest increase in tussock growth, with nitrogen addition significantly further increasing DM production. Calcium, magnesium, potassium and sulphur had only minor effect. In the absence of applied P, all the above nutrients had little effect.

Soil carbon was highly correlated with tussock biomass on unamended soils showing the fundamental importance of the soil organic regime in the mineral nutrition of fescue tussock. Mineralization of organic N and P is probably the principal factor of importance. High exchangeable aluminium levels are suspected to partially inhibit fescue growth.

Fescue tussock populations from Puffers Stream and Craigieburn differed in edaphic response, strong evidence for ecotypic differentiation. The Puffers Stream population, occurring in a less leached and slightly more fertile environment than the Craigieburn population, showed nutrient response patterns with affinities to high-fertility adapted plants whereas the converse was true for the Craigieburn population.

SECTION 3 : FESCUE TUSSOCK GRASSLAND AGRONOMY

Plate 6.1 *Lotus pedunculatus* cv ' Grasslands Maku'

CHAPTER 6: PHOSPHATE RESPONSE OF *LOTUS PEDUNCULATUS* AND *TRIFOLIUM REPENS* ON A SEQUENCE OF FIVE HIGH COUNTRY YELLOW BROWN EARTH SOILS.

6.1 INTRODUCTION

There are over three million hectares of upland and high country yellow brown earth soils which remain as one of New Zealands largest undeveloped resources. These soils experience seasonal moisture deficits and are severely nutrient deficient, principally in nitrogen (N), phosphorus (P) and sulphur (S) and also have sufficiently high aluminium (Al) levels to depress production (Sinclair and McIntosh 1981 1983, Edmeades and Wheeler 1985). Cultural amendment uses symbiotic N fixation by pasture legumes to supply N, with their P and S requirements being met, by fertiliser (O'Connor 1967, Hoglund *et al.* 1979, Ball *et al.* 1982). White clover (*Trifolium repens*), and in particular the cultivar 'Grasslands Huia', hereafter referred to as clover, is by far the most important legume used in this role throughout the country (Levy 1970, Smetham 1977, Caradus 1986a).

However the clover-grassland system is highly dependent on phosphatic fertiliser input. Traditional sources of inexpensive high quality phosphate deposits from Christmas Island, Ocean Island and Nauru are approaching exhaustion (Cook 1983). The economics of increasing fertiliser costs, current and future, necessitate change in high country grassland strategies (Floate *et al.* 1987). Though *T. repens* has a wide ecological amplitude, ranging from acidic to intermediate pH soils it is only common on moderately acidic (pH 5.6 - 6.5) soils (Grime and Lloyd 1973). Other legumes can tolerate greater acidity and lower phosphorus availability. One of the most promising of these is larger birdsfoot trefoil *Lotus pedunculatus* Cav. (syn. *L. uliginosus* Schk.; Plate 6.1).

In its natural habitat *L. pedunculatus* thrives on wet, poorly drained low fertility sites with pH ranging from 4.5 to 5.5 (Norris 1956). *L. pedunculatus* cv 'Grasslands Maku', hereafter referred to as lotus, was bred in New Zealand for increased establishment, seedling vigour and cool season production (Armstrong 1974). Evaluation of lines within both species still continues (Carradus 1986b, Keoghan and Burgess 1987).

In an important trial on an intensively cropped lowland soil Brock (1973) found lotus to outyield clover by 43% at a rate of 25 kg P ha^{-1} though clover was 12% higher yielding at 125 kg P ha^{-1}. Nordmeyer and Davis (1977) showed lotus production 3 to 10 times greater than clover on acidic high country subsoils. Lowther (1980) reported yields 4 times those of clover in Otago tussock grasslands. Lotus superiority in herbage production has been widely demonstrated in other field, glasshouse and solution culture experiments (Lambert *et al.* 1974, Crush 1974, Mears 1975, Gibson *et al.* 1975, Lowther 1977, Hall and Armstrong 1977, Caradus 1980, Lowther 1980, Morton 1981, Davis 1981a,b,c, Haynes and Ludecke 1981b, Kee 1981, Lucas *et al.* 1981, Hart *et al.* 1981a,b, Hart and Jessop 1983, McIntosh *et al.* 1984). This is generally attributed to the greater efficiency of lotus in P extraction and metabolic use, and its tolerance to acidity and phytotoxic elements, principally aluminium.

Where soil fertility is higher, or moisture deficits are limiting or frosting is severe then clover may give higher yields or rankings may vary (Scott *et al.* 1974,

Clifford 1975, Musgrave 1977a, Sheath *et al.* 1977, Floate *et al.* 1985, Scott and Covacevich 1987).

Nitrogen fixation capability of lotus appears similar that of clover. Brock (1973) reported annual fixation rates between 410-590 kg N ha^{-1} depending on P level. In the high country this fell to between 100 - 140 kg ha^{-1} $year^{-1}$ (Nordmeyer and Davis 1977). Lotus nodulation is less affected by soil acidity, though it sometimes increases with broadcast lime (Greenwood 1961, Lowther 1980, 1983, Scott and Mills 1981, Lowther and Littlejohn 1984).

As a pasture legume lotus is similar to, or slightly lower than clover in palatability and digestibility (Jones *et al.* 1970, Jones and Lyttleton 1971, Ross and Jones 1981, Ulyatt *et al* 1977, John and Lancashire 1981). Furthermore lotus does not cause bloat and it is more resistant to grass grub (*Costelytra zelandica*) and porina (*Wiseana cervinata*) (Farrell and Sweeney 1972, 1974, Farrell *et al.* 1974, East 1978).

Lotus appears intolerant of close grazing on high fertility soils in the Manawatu (Brock and Charlton 1978) and Invermay (unpublished data cited in Scott and Mills 1981) though Scott and Mills (1981) and Sheath (1981) consider that it will persist under close continuous grazing on acid soils. Poor production and persistence in improved grazed pastures has been attributed to its slow recovery from close defoliation (Sheath 1978, 1980, 1981).

In short, it has been clearly established that lotus is one of the best legumes available for highly acidic (pH 4.5 - 5.0) soils, and clover for higher fertility (pH 5.9 - 6.5) areas. Yet field data for intermediate soils (pH 5.0 - 5.8), covering over 1.8 million hectares is sparse, and inconsistent (compare Lucas *et al.* 1981 and Davis 1981d). It is also unclear whether the poor performance of lotus relative to clover as fertility increases is due to edaphic conditions favouring clover or the inability of lotus to survive grazing. The increased cost of phosphatic fertilisers, and certain future price rises, necessitate comparison of more precise response curves for both legumes to establish the optimum economic fertiliser rate rather than simply maximum yield. Though soil fertility has long been recognised as a primary factor determining yield to date there has been no field study rigorously attempting to investigate the relationship between species yield and a comprehensive set of soil chemical data that has not been confounded by climatic differences.

Therefore this study evaluates lotus performance compared with clover on moderately acidic high country yellow brown earth soils. It clarifies the understanding of edaphic factors and by examining P response curves against a sequence of soil development. The soils selected are representative of a wide range of soils throughout the eastern South Island high country. In particular, they span the variation in Craigieburn soils, which occuring on terraces and low angle fans have high potential for development. The working hypotheses was :

Lotus herbage production will be greater than clover, the relative difference in yield being inversely related to P availability and widening with increasing soil pedological development.

6.2 MATERIALS AND METHODS

6.2.1 Experimental Design

The experimental design was a split-plot factorial with two legumes, five soils and six levels of phosphate fertiliser. Soils (Chapter 1.4) and legumes were the main plot treatments, with phosphate randomized as sub-plots. Treatments were replicated in four blocks per soil, giving a total of 240 plots. The specific treatments were:-

(A)	Legumes	Trifolium repens cv. 'Grasslands Huia' Lotus pedunculatus cv. 'Grasslands Maku';
(B)	Soil	Puffers Creek terraces one to five, T1 - T5
(C)	Phosphate	0.0, 12.5, 25.0, 50.0, 100.0, 400.0 kg P ha^{-1}.

Each block was 7.20 x 4.20 m separated by a 1.0 m walkway from the adjacent block. Blocks were subdivided into two legume main plots of 7.20 x 2.00 m. Each legume main plot was subdivided into six 2.00 x 1.00 m subplots with a 20 cm margin between plots, except on the first terrace where this was not possible. Barbed rabbit netting excluded grazing animals (Plates.1.3, 1.4).

6.2.2 Legume Culture and Establishment

Lotus and clover seedlings were pre-grown in a glasshouse to ensure good field establishment of uniform plants. Commercial seed (Prebble Seeds Ltd, Christchurch) and specific lotus and clover rhizobium inoculum (Rhizocote Peat Culture, TNL Group, Nelson) were used. Inoculum was applied at recommended rates (6 g kg^{-1} seed for both lotus and clover). Individual seeds were planted into 8 x 2.5 cm alkathene tubes filled with a (1:1) peat:sand mixture on 3 July 1981 and grown in a glasshouse. Seedlings were regularly watered with tapwater. After 8 weeks they were removed from the glasshouse to 'harden' before field planting.

Seedlings were systematically space-planted on the Puffers Stream terraces (Chapter 1) between 3 - 19 November 1981. Ten clover and five lotus seedlings per plot were planted on each terrace on the 3rd and 4th November and a further three lotus seedlings per plot were planted on the 19th November. A 1 x 1 m steel quadrat, subdivided by string into nine 33.3 x 33.3 cm grids, was used to determine the planting position for each 2 x 1 m subplot (Plate 6.2).

Seedlings were planted in the centre of the grids, except in a few cases where they were offset because of obstruction. After removing a soil core (ca. 9 x 2.5 cm) the seedling and soil were gently pushed from the tube, inserted into the hole and watered.

Each plant was checked for survival 1 month after planting on 4 December 1981 and as an extra precaution to ensure effective nodulation a further 2-5 ml of inoculum was applied in aqueous suspension to the base of each seedling. On 12 December 131 clover seedlings, almost all suckling clover contaminants, and 22 lotus seedlings were replaced with seedlings which had been left unplanted on the site. Mortalities were hereafter treated as treatment effects.

6.2.3 Fertiliser Application

Six phosphate treatments, designated P0 to P400, were applied at rates per plot equivalent to 0.0, 12.5, 25.0, 50.0, 100.0, and 400.0 kg of phosphorus per hectare. Disodium dihydrogen pyrophosphate ('Aerophos') was used as the phosphate source, with the following analysis specifications:-

		Specification Limit	Typical Assay (%)	(%)
$Na_2 H_2P_2O_7$		97.0	min	98.0
Heavy metals		10 ppm max	-	
Particle size + 60 B.S.S.	0.5	max	0.2	
Particle size + 100 B.S.S.	0.5	max	1.5	
Moisture		0.5	max	

(ICI New Zealand Ltd, pers. comm.)

Basal fertilisers at the following rates were applied at the same time as treatment fertilisers:-

Fertiliser (Analar grade)	Form	Rate (kg ha-1)	Elemental rate (kg ha-1)	
Gypsum	$CaSO_4$	20	Ca 5.89	S 4.71
Potassium sulphate	K_2SO_4	50	K 22.44	S 9.20
Magnesium sulphate	$MgSO_4.7H_2O$	100	Mg 20.19	S 26.64
Sodium molybdate	Na_2MoO_4	0.4	-	
			Total S	40.55

Fertilisers were evenly spread by hand between 19 November 1981 and 4 December 1981. Application was only made when conditions were calm. Molybdenum was sprayed on in solution. Plots were lightly watered after fertiliser application to prevent subsequent wind removal.

6.2.4 Assessment of Survival and Production

Legume aerial biomass was estimated by visual scoring and harvest from September 1982 to March 1985. Plants were first scored towards the end of summer, three months after planting (9 February 1982). During the second season they were assessed in early spring and summer (16 September 1982; 22 December 1982) and harvested at the beginning of autumn (12 March 1983). They were then scored the following autumn (25 March 1984) and finally in late summer the following year (18 Febrary 1985). Scoring in 1984 and 1985 was correlated with herbage production by harvesting the plots after scoring on the fourth terrace, T4.

At each assessment live plants were ranked on a 10-point scale and missing or dead plants were recorded. The largest plant of each species was given a score of 10 and the smallest a score of 1, estimated in relation to the 33.3cm square grids on a 1 x 1 m steel quadrat (Plate 6.2). All other plants were located, and scored using the grids as a scale. For example, species were assessed in 1984 using the following scaling as a guide:

SCORE	LOTUS	CLOVER	
D or M	Dead or Missing	Dead or Missing	
1	1- 2 stems; < 15 cm height	< 10% cover*	
2	2- 3 stems; < 15 cm height	10 < 25% cover	
3	3- 5 stems; < 25 cm height	25 < 40%	
4	5- 8 stems; < 30 cm height	40 < 50%	
5	8-10 stems; 30-40 cm height	50 < 60%	< 50% cover
6	8-10 stems; + 40 cm height	60 < 75%	> 50% cover
7	> 10 stems; 40-50 cm height	75 < 90%	50- 75% cover
8	Many stems; + 50 cm height	90 <100%	75- 85% cover
9	Many stems; 50-60 cm height	100 + 33%	85-100% cover
10	Many stems; + 60 cm height	100 + 66%	100+ % cover

* Cover: "The proportion of ground occupied by perpendicular projection on to it of the aerial parts of an individual plant" (Greig-Smith 1964, 1983).

Individual lotus plants could be scored relatively easily, but by the fourth assessment (12 March 1983) it was impossible to differentiate individual clovers in all cases. Therefore all the legume herbage in the grid in which the original plant occurred was scored. Herbage in adjacent grids that were not planted were divided equally between the nearest planted grids.

Scoring error was assessed by comparing scores from two independent observers. One observer (myself) scored every assessment, joined with a second observer on 9 February 1982, 2 March 1983 and 25 March 1984. Any scores differing by two units or more between observers were reassessed immediately after scoring each block. Differences greater than two units were always adjusted in this way. Differences of two units were adjusted at the discretion of the observer.

Plots were harvested at the end of the second season (March 1983). Prior to this no destructive yields were taken, to allow full establishment of the trial.

Plants in each subplot were cut about 1 cm above ground level using hand clippers or an electric trimmer or were hand plucked. Terrace five was first visually scored and every lotus plant was individually harvested while clover was bulked per plot. Both legumes were bulked per plot on the remaining terraces. In the third (1983-84) and fourth seasons (1984-85) all plots on terrace four were harvested for correlation with visual scores.

Harvested samples were transported to Lincoln in plastic bags within 14 hours and stored in a coolstore at 1.5 °C (range 1-3 °C). Legumes were botanically dissected from other plants as quickly as possible to minimize weight loss through respiration during storage. Dissection took 8 days for the largest harvest (1983). Large clover samples were subsampled before dissection. Samples were thoroughly mixed and successively quartered until a subsample size of roughly 150-200 g fresh weight was obtained. All legume samples from harvests in subsequent seasons were completely fractionated. Samples were oven dried in a large force-draught oven at 80 °C for 24 hours (Allen 1974, Appendix 6.1) and weighed to an accuracy of $\pm$ 0.1 g.

Plate 6.2 1 x 1 m quadrat used for space-planting and scoring, grids 33.3 cm^2.

6.2.5 Chemical Analysis

Oven dried samples were cut into 2-3 cm lengths, mixed and quartered (Allen 1974), ground in a hammer mill to pass a 1 mm sieve, and a sub-sample of 5-10 g was stored in a plastic vial for analysis. Nitrogen and phosphorus were then determined colourimetrically following H_2SO_4: H_2O_2 wet acid digestion (Appendix 6.2).

6.2.6 Statistical Analysis

Analysis of variance using the general statistics package GENSTAT (Alvey *et al.* 1982) tested the significance of treatment effects. The validity of the assumptions required for ANOVA were checked by plotting residuals against fitted values (Alvey *et al.* 1982, p.93) and CSIRO macro sub-routines (Alvey *et al.* 1983).

Non parametric analysis, specifically Spearman's rank correlation, was used when comparing visual scores by observers. This test did not require differences between adjacent visual score units to correspond to equal differences in cover. Furthermore, it required no prior assumption of population normality.

Significance levels throughout the text are indicated as follows:

*** = $P < 0.001$; ** = $P < 0.01$; * = $P < 0.05$; NS = $P > 0.05$.

6.3 RESULTS

6.3.1 Yield Estimation by Visual Score

Visual scoring differences between observers were small. In 1983 0.5% of lotus and 0.8% of clover scores differed by three units between observers and 4.2% of both legumes differed by two units. No lotus scores differed by three units in 1984, and only 3.5% differed by two units.

No significant bias in scoring between observers occurred in any season. Spearman's rank test showed a highly significant correlation between observers (rho = 0.963 - 0.983). With the regression analyses, as expected if there was no difference, regression coefficients were close to unity and intercepts close to zero.

Visual scores were reasonable estimators of dry matter yield for both legumes. The actual relationship was curvilinear as scoring underestimated dry matter for large plants (Fig. 6.1). Therefore square root and $\log_{10}$ transformations were used in fitting equations to convert scores into estimates of yield:

LOTUS

1984	SQRT DM	=	-17.380	+	5.209	X	(r = 0.950)
1985	SQRT DM	=	0.022	+	3.632	X	(r = 0.857)

CLOVER

1984	SQRT DM	=	-0.714	+	3.332	X	(r = 0.951)
1985	SQRT DM	=	-37.28	+	40.55	X	(r = 0.965)

where DM = dry matter yield per plot
X = average visual score per plot

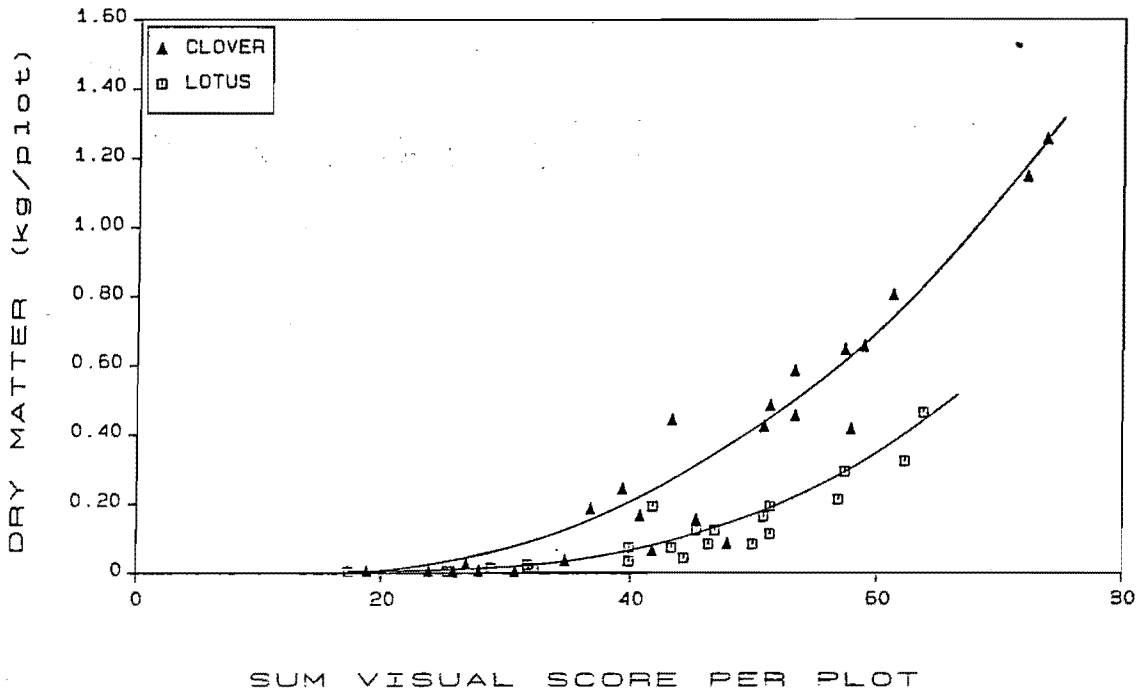


Figure 6.1 : The relationship between legume visual score and herbage DM

Estimated and actual yields for T4 against P are shown for clover (Fig. 6.2a) and lotus (Fig. 6.2b). While this is not an independent test, as the same scores were used to produce the predictive equations, it does indicate how accurately scoring estimated yield when averaged for P level.

There was little difference in the variance extracted regressing either individual plants (n=178) or summed plot (n= 23) data:

Log_{10} Plant DM	=	-1.710	+	0.680 PLANT SCORE		(r = 0.925)
Log_{10} Plot DM	=	0.562	+	0.087 PLOT SCORE		(r = 0.938)

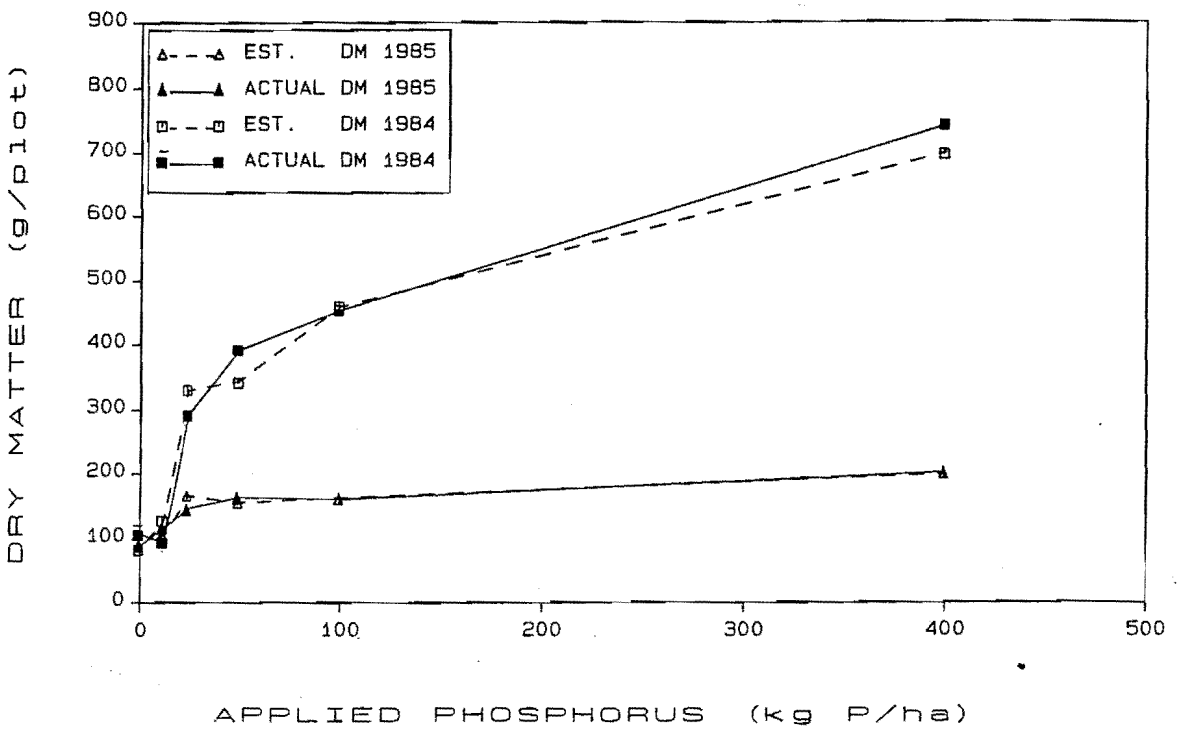


Figure 6.2a : Actual vs estimated clover DM production 1984 - 1985

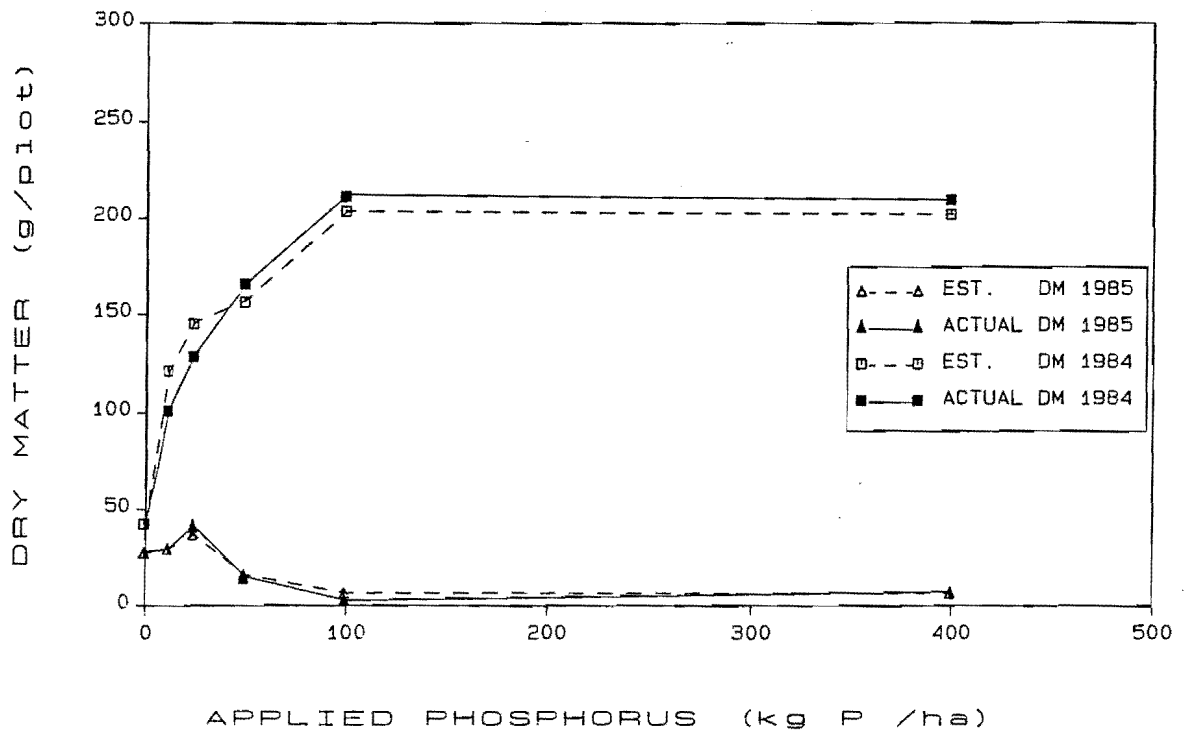


Figure 6.2b : Actual vs estimated lotus DM production 1984 - 1985

6.3.2 Seedling Mortality

Comparison of plants recorded as absent from 1983-1985 produced 23 inconsistent records for lotus (0.004% of all records) and 83 for (clover 0.014%). Each assessment was scored without reference to previous scoring to avoid bias and, as a result, some plants were recorded as present although absent in other assessments. Seventy-six percent of such anomalies for lotus and 83 percent for clover occurred on the first terrace where poor growth resulted in many small inconspicuous plants. After careful comparison of all scores, and a further field check on 15 March 1985, all anomalies were corrected. Eighteen lotus and 11 clover scores were amended from missing to present and the remainder of anomalous records from present to absent. Stolon invasion from neighbouring plants was responsible for most clover mis-scoring. No rigorous assessment of mortality was possible after the second season due to such confounding.

Over 96 percent clover and 87 percent lotus seedlings survived the first summer. After winter, survival dropped to 92 and 83 percent respectively and by mid summer only a further 0.4 percent clover and 0.7 percent lotus died (Table 6.1). Assessments in the following seasons showed no further mortality for either legume. Though this was confounded by invasion from neighbouring plants, no plants were observed dead and the actual mortalities were probably extremely low (< 0.1%).

Table 6.1: Mortality of 1920 lotus and 2400 clover seedlings on T1-T5 3 to 13 months after transplanting on 3 November 1981

TERRACE	CLOVER				LOTUS			
	9/2	16/9	22/12	TOT	9/2	16/9	22/12	TOT
T1	28	33	5	66	97	33	4	134
T2	8	7	0	15	11	1	0	12
T3	5	1	0	6	7	1	2	10
T4	1	3	0	4	5	2	1	8
T5	4	2	0	6	19	1	1	21
TOTAL	46	46	5	97	139	38	8	185

Mortalities were significantly higher for both legumes on the first terrace than on all others ($p<.001$). Sixty-eight percent of all clover mortalities and over seventy two of percent of all lotus deaths occurred on T1 (Table 6.1).

Phosphate application had no significant affect on legume mortality (Table 6.2). The soil x P interactions were not significant.

Table 6.2: Total lotus and clover mortalities at six levels of P 3 and 11 months after establishment 1982 (summed across T1-T5).

Legume	Date	Phosphate level (kg ha) 0	12.5	25	50	100	400	F ratio
CLOVER	9/2	7	7	5	7	10	10	0.606 NS
	16/9	7	12	10	6	6	5	0.615 NS
LOTUS	9/2	24	24	28	22	14	28	0.688 NS
	16/9	8	5	8	6	6	5	0.278 NS
TOTAL		**46**	**49**	**51**	**41**	**36**	**46**	

6.3.3 Herbage Production

Summarized analysis of variance results for $\log_{10}$ transformed dry matter yields 1982-85 are presented in Tables 6.3 and 6.4.

Table 6.3 Three-way factorial analysis of variance of $\log_{10}$ transformed DM yield $plot^{-1}$ on five soils T1-T5, 1982-85 (Sums of Squares %).

Source of Variation	1982-83 S.S%	p	1983-84 S.S%	p	1984-85 S.S%	p
Legume	13.7	***	5.7	***	67.7	***
Phosphate	38.0	***	29.0	***	0.9	*
Terrace	42.9	***	24.3	***	11.3	***
Terrace. x Legume	4.7	***	12.1	***	1.9	*
Terrace. x P	6.2	***	3.5	NS	1.6	NS
Legume x P	1.5	***	1.2	NS	5.3	***
Terrace. x Legume x P	2.0	**	5.7	**	1.1	NS

Table 6.4 Three-way factorial analysis of variance of log10 transformed DM yield plot^{-1} on four soils T2-T5, 1982-85 (S.S%.= Sums of Squares %).

Source of Variation	1982-83 S.S.%	p	1983-84 S.S.%	p	1984-85 S.S.%	p
Legume	9.9	***	15.6	***	67.7	***
Phosphate	67.4	***	37.3	***	0.9	*
Terrace	3.4	**	11.9	***	10.9	***
Terrace. x Leg.	1.0	NS	7.2	***	1.9	*
Terrace. x P	4.9	***	3.3	NS	1.6	NS
Leg. x P	1.6	***	3.4	***	5.3	***
Terrace. x Leg. x P	1.1	NS	0.9	NS	1.1	NS

The tables show treatment factors accounted for 80 to 90% of the variability in yield over the three seasons (i.e. the % sum of squares in the ANOVA models). Phosphate had the major effect on yield but the legumes differed in response and this depended on both P level and terrace, i.e., there were strong second order interactions. The significant three factor, terrace x Legume x P, interaction was due to inclusion of the first terrace. The interaction disappeared when T1 was dropped from the data set used for analysis (Table 6.4). Soil morphology and water holding capacity of T1 were grossly different from all other soils (Chapter 1.4). Main effects and interactions are discussed in the following sections.

6.3.3.1 Legume production 1982-85

By late summer of the first season (9 February 1982) lotus mean visual score, averaged across all soils and P treatments, was greater than clover (4.4 vs. 3.6; p <.001). However, by next spring (16 September 1982) this was reversed (clover 3.0 vs lotus 1.7, p<.001) with the difference being maintained through early summer (22 December 1982 : 4.7 vs. 3.4, p <.001). At the end of the season (12 March 1983) clover produced 2.9 times more dry matter (DM) than lotus (Table 6.5).

Table 6.5 Average Legume dry matter yield 1982-85 (g DM plot^{-1})

LEGUME	82-83	83-84	84-85	TOTAL
CLOVER	350	110	25	488
LOTUS	120	220	170	510
TOTAL	**471.8**	**339.2**	**191.2**	**1000**
SEM	16.0	7.2	5.0	-
F	***	***	***	-

Maximum lotus production did not occur until the following 1983-1984 season, DM yield being 1.9 times greater than clover, though only 63% of the maximum clover yield in the 1982-1983 season. Yield of both legumes decreased in 1984-85 notably clover which dropped by 79.2% compared with a decline of only 24.9% in lotus production.

6.3.3.2 The effect of phosphate on production

Terrace one differed ($p < .001$) from all other terraces and was unique in that both legumes showed almost no response to P at any season (Table 6.6).

Table 6.6 Legume response to applied phosphorus on T1 1982-85

(a) Average Visual Score per Plant

Date	Legume	Applied P (kg P ha-1) 0	12.5	25	50	100	400	SEM
9. 2.82	Clover	1.47	1.43	1.47	1.50	1.36	1.89	0.18
	Lotus	1.45	1.29	1.42	2.02	2.00	2.09	0.20
16. 9.82	Clover	1.03	1.00	1.06	1.25	1.10	1.60	0.17
	Lotus	1.04	0.95	0.91	0.97	1.02	1.04	0.19
22.12.82	Clover	2.22	2.57	3.09	2.30	2.23	3.53	0.19
	Lotus	1.13	1.00	0.98	1.28	1.96	1.25	0.21

(b) Dry Matter Yield (g plant -1)

10. 3.83	Clover	18.3	17.3	43.8	60.1	31.4	190.0	61.9
	Lotus	16.0	17.7	26.1	11.0	8.8	17.0	55.1
25. 3.84	Clover	30.7	25.5	88.9	129.4	64.2	215.9	57.4
	Lotus	14.9	70.1	25.8	22.5	31.3	18.9	57.4
24. 2.85	Clover	12.8	14.0	11.2	9.9	5.8	6.9	19.1
	Lotus	60.4	129.5	65.5	78.2	136.5	148.6	19.1

In contrast, legume production on the four upper terraces was highly responsive to the rate of applied P in every season (Table 6.4). Therefore T1 was dropped from the data set used for the subsequent analysis of legume P response.

Three months after planting (9 Febrary 1982) both legumes gave highly significant responses to applied phosphate ($p < .001$). Clover responded strongly up to P50 with only slight increases to P400 while lotus responded most strongly at lower P rates (P0 to P25) and gave no significant response above P100 (Fig. 6.3).

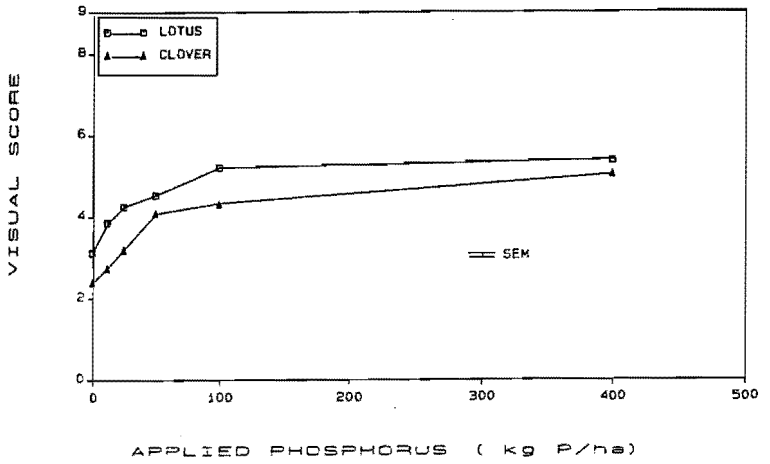


Figure 6.3 : The effect of applied P on legume herbage production three months after planting (9/2/82)

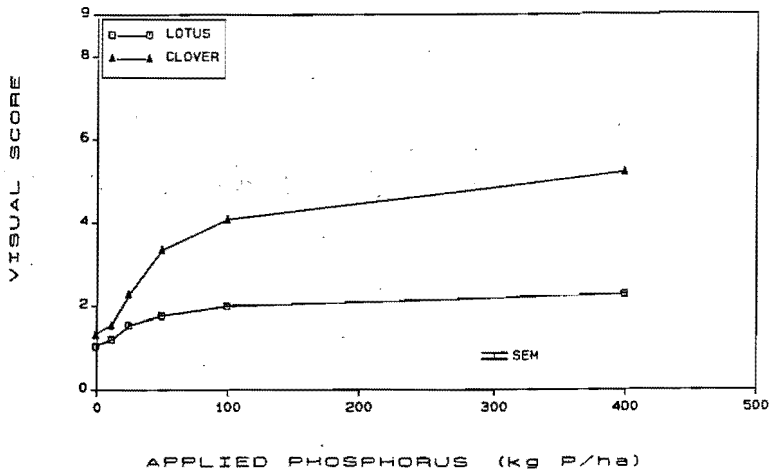


Figure 6.4a : The effect of applied P on legume herbage production ten months after planting (16/9/82)

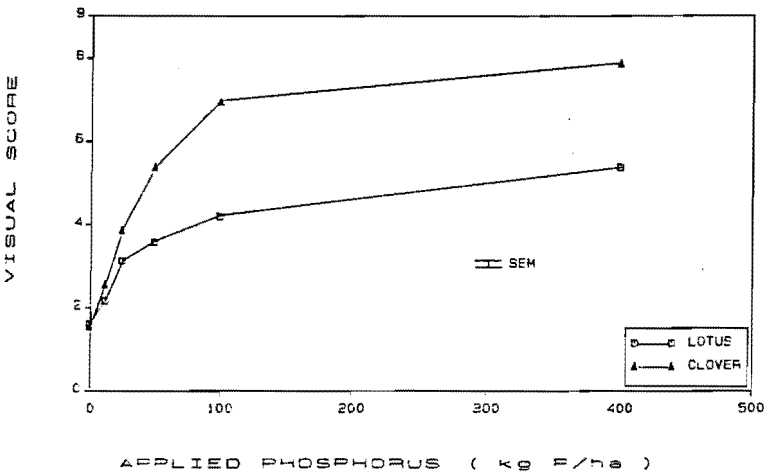


Figure 6.4b : The effect of applied P on legume herbage production thirteen months after planting (22/12/82)

Spring and summer visual scores the next season (16 September, 22 December 1982) showed a similar pattern (Figs. 6.4a,b). In both cases clover response was greater than lotus between P25 to P100 causing the highly significant legume by P interaction. Total season DM response curves in autumn continued to show a similar pattern (Fig. 6.5a). Relative clover response to P was greater than lotus, increasing 25.3 times between P0-P400 for clover compared with 14.1 times for lotus. As before, the greatest difference between the two legumes occurred between P25 to P100. At lower P rates, (P0 to P25) clover yields were only 1.5 and 2.5 times greater than lotus compared with 3.5 and 3.2 times at P50 and P100. The difference lessened to 2.7 times greater yield at P400.

In contrast with the 1982-83 season, lotus response in 1983-84 was greater than clover (Fig. 6.5b). Yield increased 8.5 times between P0-P400 against a 3.5 times increase in clover production. Furthermore, the difference in performance increased with increasing P levels to a maximum of 3.0 times greater yield of lotus at P400. This caused a highly significant legume by P interaction (Table 6.4).

The greatest divergence between the legumes, both in total yield and response to P, occurred in 1984-85 (Fig. 6.5c). Lotus, as previously, responded positively to P approximately doubling production between P0 and P400, with the greatest response between P0 - P25. Clover, however, showed no significant difference in yield between P0 - P50 and a negative response at higher P rates. Production at P400 was less than half the yield at P0.

6.3.3.3 The effect of terrace on production

Terraces had a highly significant effect on herbage production in every season (Tables 6.3 and 6.4). Comparison of the change in percentage sum of squares between these tables shows the effect of the removal of T1 on variability due to terraces. Terrace one alone accounted for 33.0% of the variability in 1982- 83 and 12.4% in 1983-84, second only to the main effect of P in both years.

Herbage production from each terrace is summarized from 1981-85 in Table 6.7. Terrace one consistently gave the lowest production in every season. Dry matter yield in 1982-83 was nearly 6.6 times greater than T1 on T2 and T3 and 10.7 times greater on the highest yielding terrace, T4. Production on T5 was similar to, but slightly lower than, T2. The same pattern of production occurred in 1983-84 except that differences between terraces were smaller - T4 yield was only 3.7 times greater than T1.

Differences in production between terraces narrowed even further in 1984-85 and the relative performance changed. T3 gave the highest yield, though only twice the yield of T1. T2 did not differ significantly from T3, nor T4 from T5.

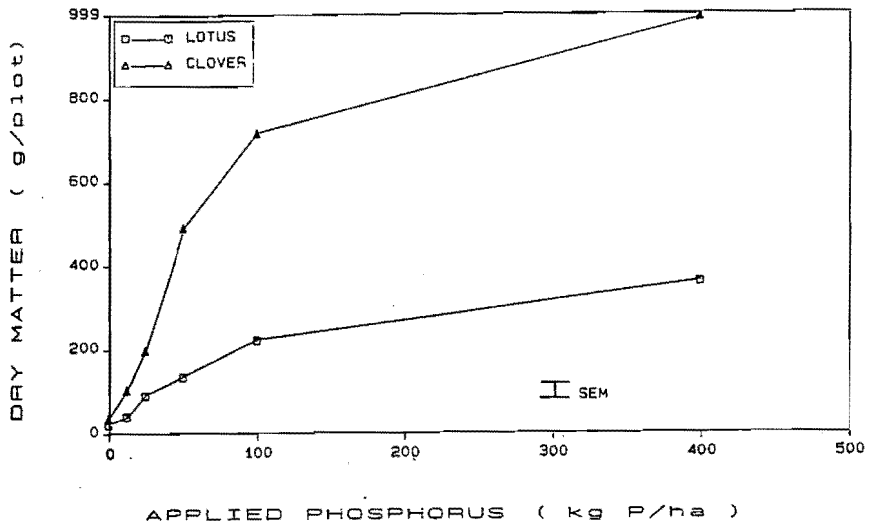


Figure 6.5a: The effect of P on mean legume DM production 1982-1983

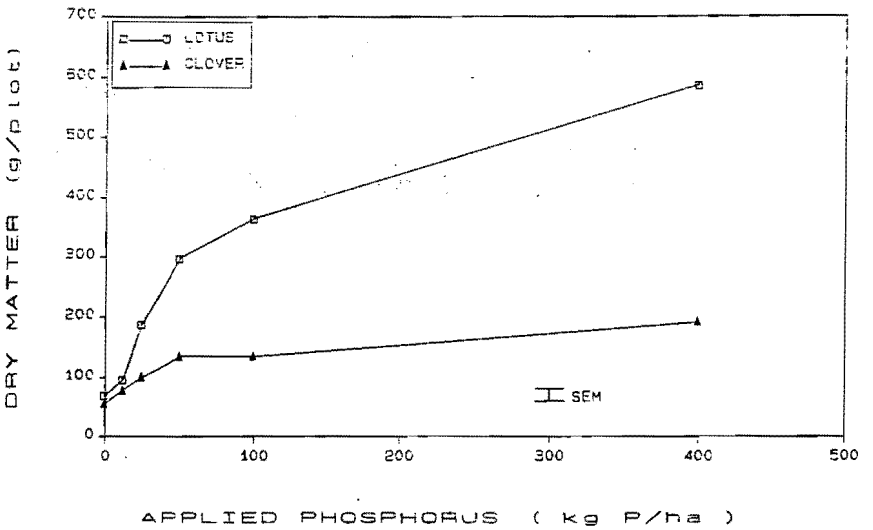


Figure 6.5b: The effect of P on mean legume DM production 1983-1984

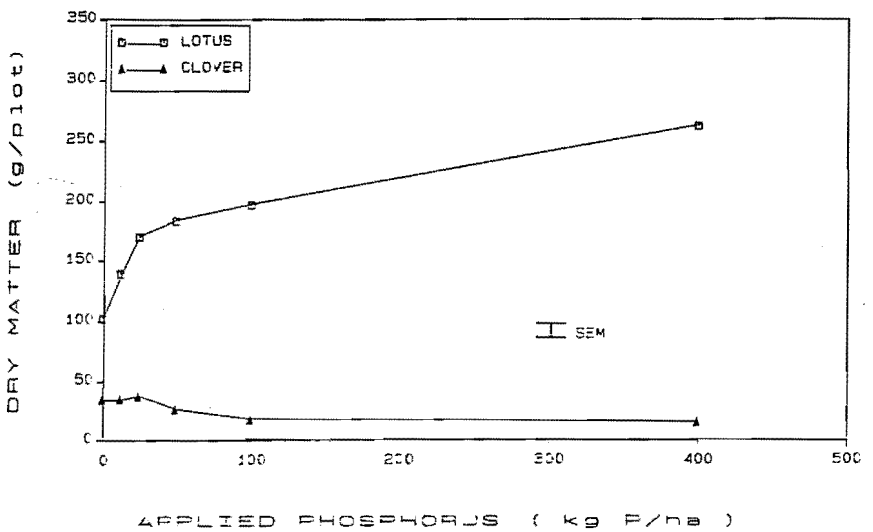


Figure 6.5c: The effect of P on mean legume DM production 1984-1985

Table 6.7 Average lotus and clover herbage production on T1-T51982-85 (visual score and dry matter yield per plant)

Date	Legume	Terrace T1	T2	T3	T4	T5	SEM	F
(a) Visual Score								
9. 2.82	Clover	1.5	3.4	3.2	4.5	3.4	0.07	***
	Lotus	1.7	3.8	4.1	5.2	4.5	0.08	***
	MEAN	1.6	3.6	3.6	4.8	3.9	0.04	***
16. 9.92	Clover	1.2	2.6	2.4	3.1	3.8	0.08	***
	Lotus	1.0	1.3	1.3	1.9	2.2	0.06	***
	MEAN	1.1	2.0	1.9	2.6	3.1	0.03	***
22.12.82	Clover	2.7	-	4.1	4.9	5.2	0.09	***
	Lotus	1.3	-	2.9	3.5	3.6	0.08	***
	MEAN	2.0	-	3.6	4.3	4.5	0.04	***
(b) Dry Matter Yield								
12.3.83	Clover	60.3	406.0	340.2	603.5	350.3	35.8	***
	Lotus	16.1	95.3	163.2	217.0	120.9	36.2	***
	MEAN	38.2	250.6	251.4	410.3	235.6	25.9	***
25.3.84+	Clover	119.9	189.3	74.3	140.8	56.6	23.4	***
	Lotus	30.6	219.6	266.1	340.7	245.3	23.4	***
	MEAN	75.3	204.4	170.2	240.8	150.0	16.6	***
24.2.85+	Clover	10.1	40.7	36.9	20.9	12.9	7.8	***
	Lotus	103.1	199.0	208.5	147.3	169.3	7.8	***
	MEAN	56.6	119.9	122.7	84.1	91.1	5.5	***

+ Dry matter yields estimated from scores (Section 6.3.1)

Terraces influenced how legumes responded to rate of applied P as indicated by the significant second order interactions between terrace and legume and terrace and phosphorus (Tables 6.3 and 6.4). Removal of T1 made the legume x terrace interaction non significant in 1982-83 but in other seasons only reduced the variance due to both interactions.

The legume x terrace interaction in 1982-83 was due to disproportionately lower lotus production relative to clover on T1 (Tables 6.8). The following season 40.5% of variance due to the interaction was directly attributable to this cause, but when removed, the interaction remained highly significant due to the high lotus yield relative to clover in T3 and T5. The interaction in 1984-85, though weaker, was again due to differential performance on T1 and T5 (Table 6.8).

Table 6.8. Interaction between legume and terrace 1982-85 (g DM/plot)

	1982 - 1983			1983 - 1984			1984 - 1985		
Tce	Clover	Lotus	L:C	Clover	Lotus	L:C	Clover	Lotus	L:C
1	60.3	2.5	0.04	92.4	39.0	0.4	10.1	110.2	10.9
2	406.0	95.3	0.23	185.7	219.6	1.2	40.7	199.0	4.9
3	340.2	163.2	0.48	73.7	266.1	3.6	36.9	208.5	5.7
4	603.5	217.0	0.36	149.7	340.7	2.3	20.9	147.3	7.1
5	350.3	120.9	0.35	54.3	245.3	4.5	12.9	169.3	13.1

The interaction between terrace and P was only significant in 1982-83 (Tables 6.3 and 6.4). Terrace one accounted for 25.6 of the variance attributable to the interaction but when removed the interaction remained highly significant (Table 6.4). This was due to the higher yield on T2 at low P levels relative to other terraces and the proportionately greater increase of T5 yield at P400 (Fig. 6.6).

Clover and lotus production the first season after establishment (1982-3), averaged across all P rates per terrace, decreased as the proportion of resident grasses browntop (*Agrostis tenuis*) and sweet vernal (*Anthoxanthum odoratum*) increased (Fig. 6.7). The relationships between grasses and legume yield were:

Clover DM = 758.6 - 193.6 Grass (r = 0.88)
Lotus DM = 288.6 - 80.4 Grass (r = 0.89)

where Grass is the mean cover/abundance index for browntop + sweet vernal (data : Table 1.9).

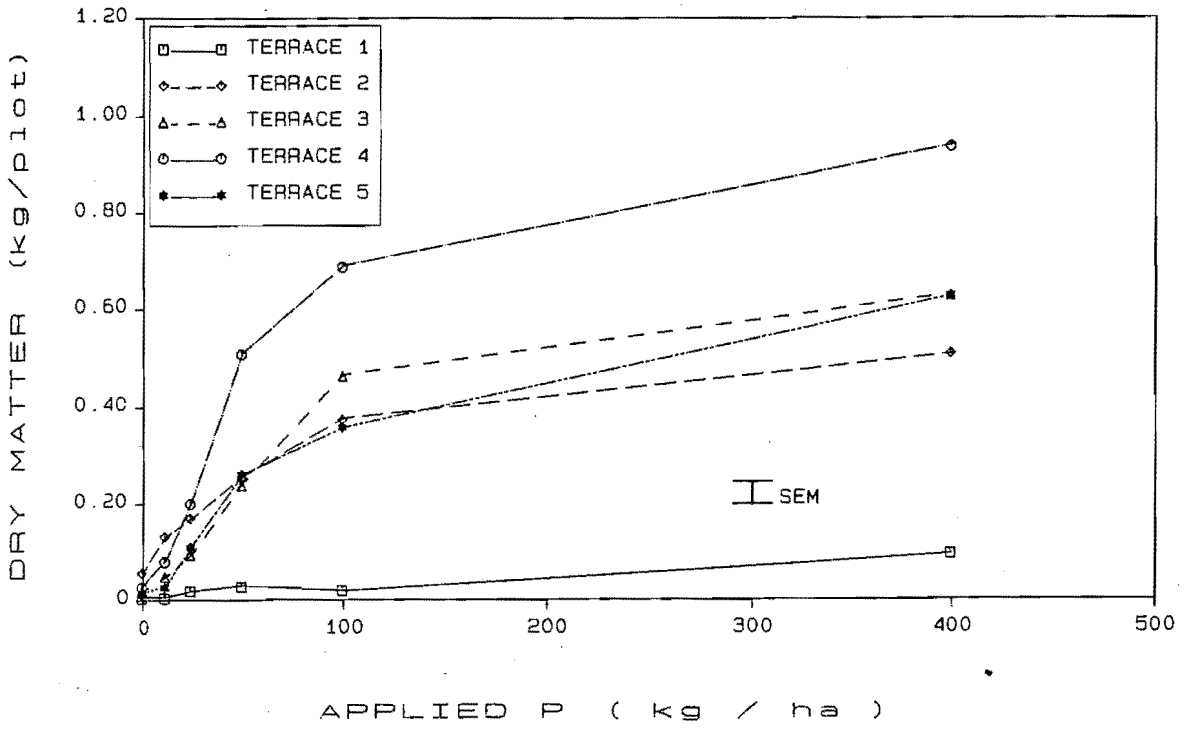


Figure 6.6 : The effect of P and soil on mean legume yield 1982-1983

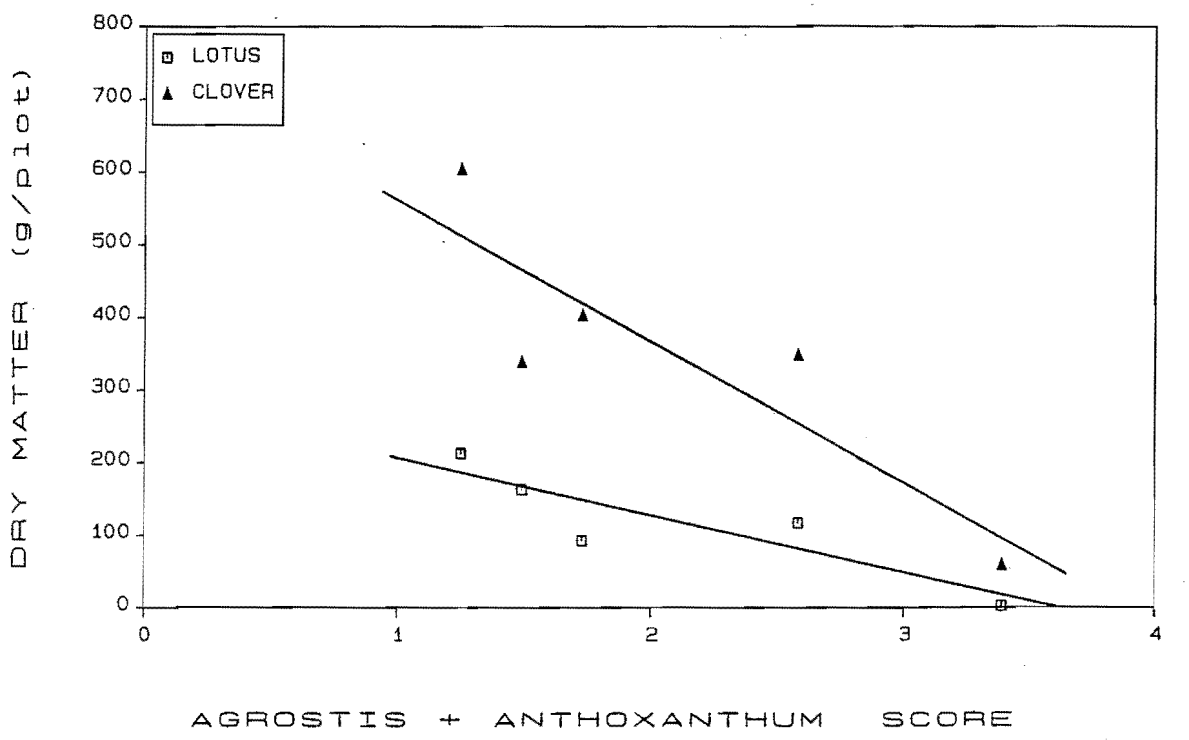


Figure 6.7 : The effect of resident grasses on mean legume production on T1-T5, 1982-1983

The soil chemical variables in T1-T5 (Appendix 2.2) that were most significantly related to herbage production without applied P (P0) are shown in Table 6.9.

Table 6.9: Correlation coefficients (r) of Legume Yield at P0 with Soil chemical variables.

Depth (cm)	Lotus			Clover			
	pH	CEC	AL_E	Ptot	Porg	Pxrf	Pap
0-10	-0.86 (.06)			.97 (.01)	.96 (.01)	.95 (.01)	.93 (.02)
10-20		.93 (.02)		.92 (.03)	.92 (.03)	.91 (.03)	.80 (.10)
20-30			.94 (.02)	.93 (.03)	.87 (.05)	.86 (.06)	.87 (.06)

where ( ) is probability level of coefficient.

Legume production at the two study sites, Puffers Stream and Craigieburn, are compared three seasons after establishment in Fig. 6.8. The Craigieburn data came from the Cave Stream terrace (CB3) in the foreground of the frontispiece (Kee 1981). Plant yields at Puffers Stream were averaged over a comparable range of P treatments on T4 for a comparison of legume performance on moderately and strongly leached Craigieburn HC YBE soils..

6.3.4 Herbage Mineral Content

Herbage phosphorus concentration (petiole + lamina) 16 month after establishment was greater in clover (1.71 mg g-1 DM) than lotus (1.42 mg g-1 DM; $p < .001$). Phosphorus concentrations increased in both legumes with rate of applied P ($p < .001$). The significant soil by legume interaction ($p < .04$) was due to lotus P concentrations being much higher on T1 relative to the other terraces than occurred with clover (Fig. 6.9).

Tissue P concentrations increased almost linearly up to 100 kg applied P ha-1 before the rate of increase lessened between P100 and P400 (Fig. 6.10). Both legumes responded similarly to applied P.

Total P uptake was 3.6 times greater in clover (598 mg $plot^{-1}$) than lotus (164 mg $plot^{-1}$; $p < .001$). P uptake differed between terraces ($p < .001$) with clover taking up proportionately more P on T2 and T4 than lotus (Fig. 6.11). Phosphate efficiency, defined as DM produced per unit applied P (Blair and Cordero 1978), was only highest in clover during the first season after establishment (Table 6.10).

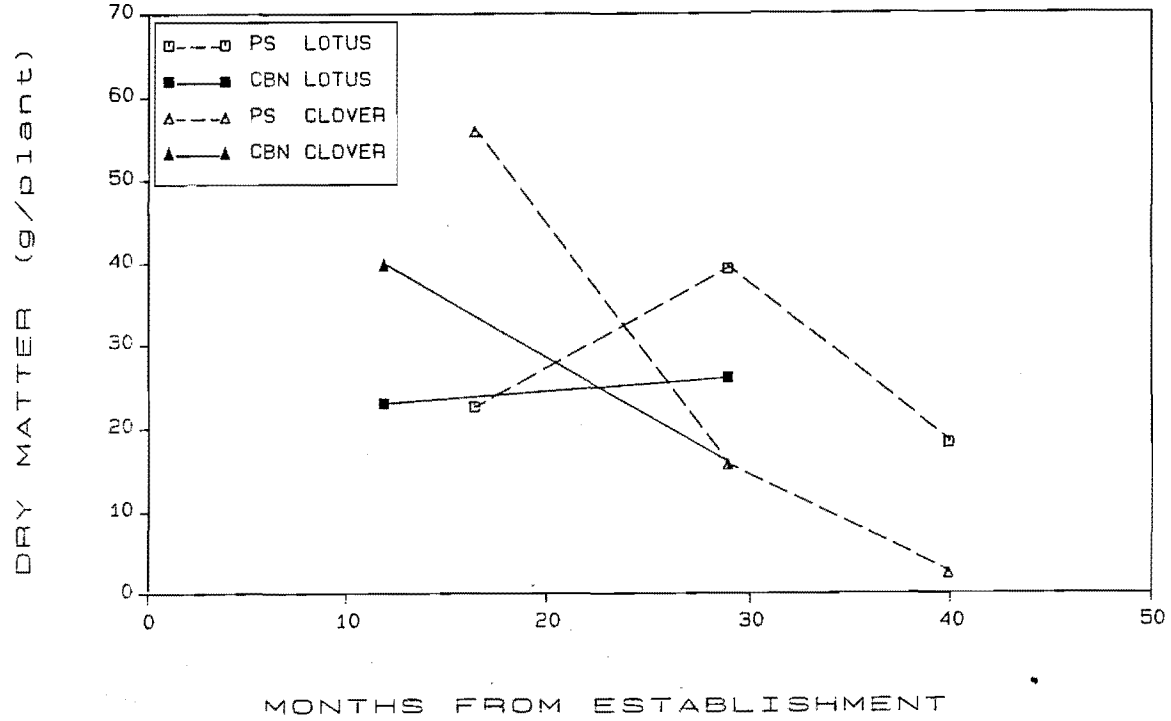


Figure 6.8 : Comparative legume production at the Craigieburn and Puffers Stream Study Sites

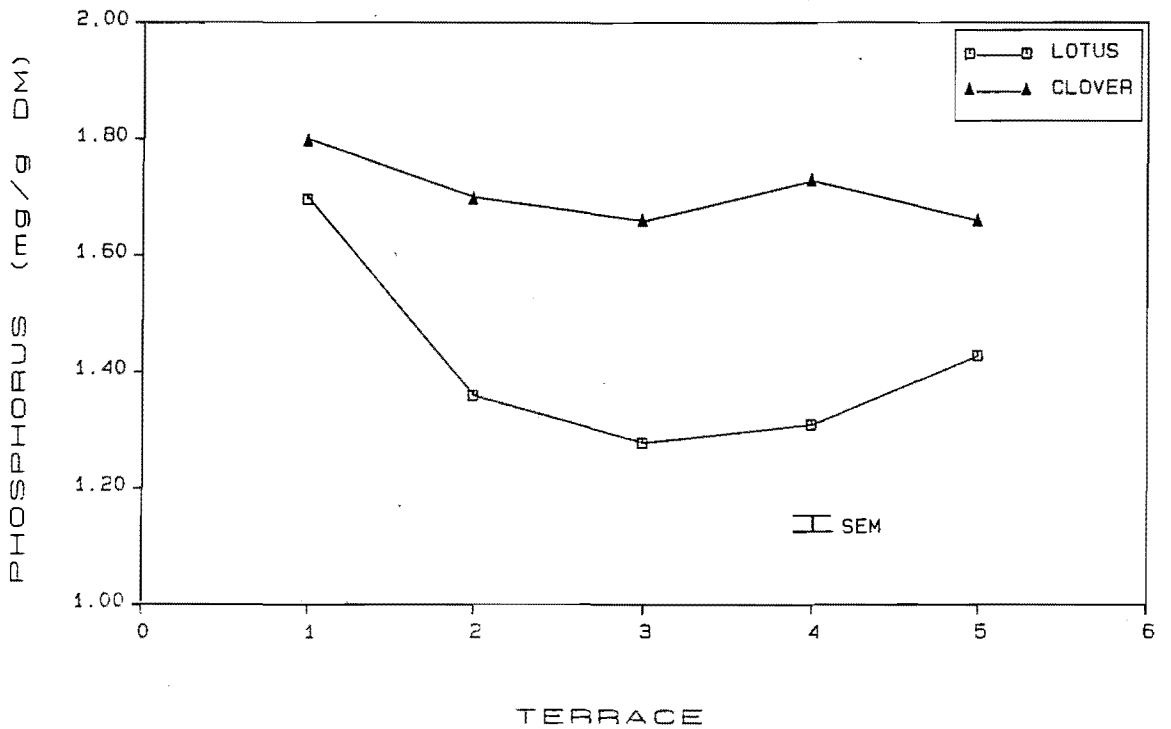


Figure 6.9 : The effect of soil on lotus and clover shoot P concentration, 1982-1983

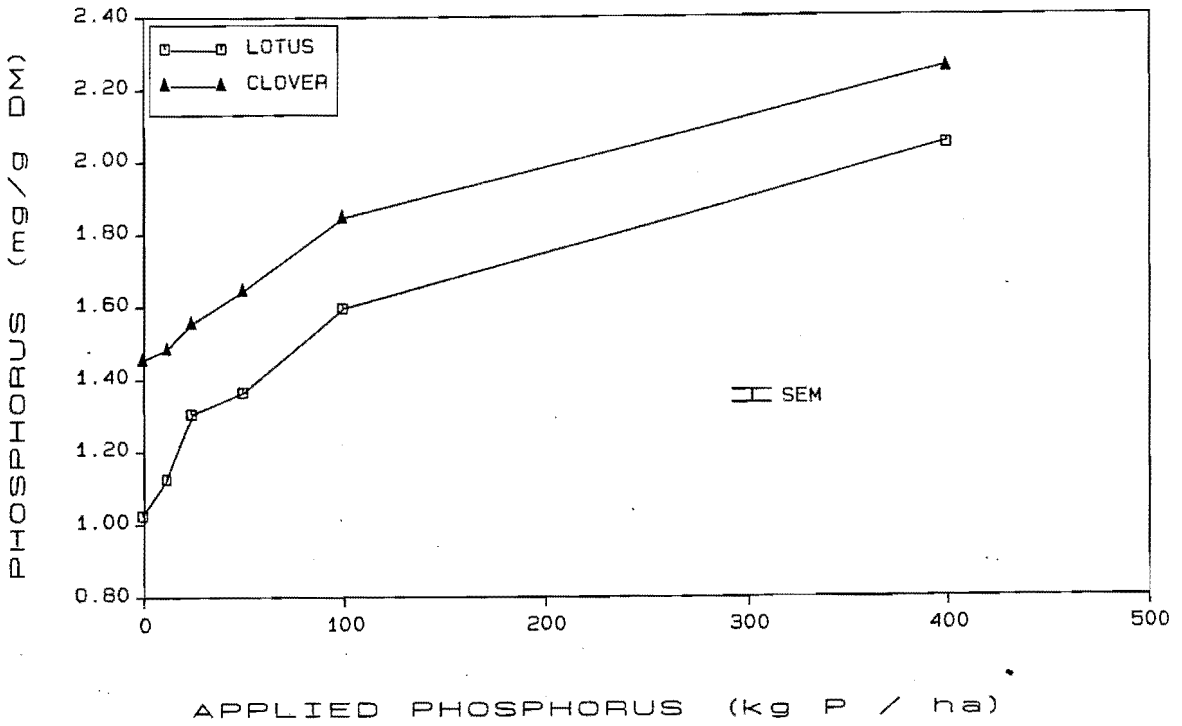


Figure 6.10 : Lotus and Clover shoot P concentrations with applied P, 1982-1983

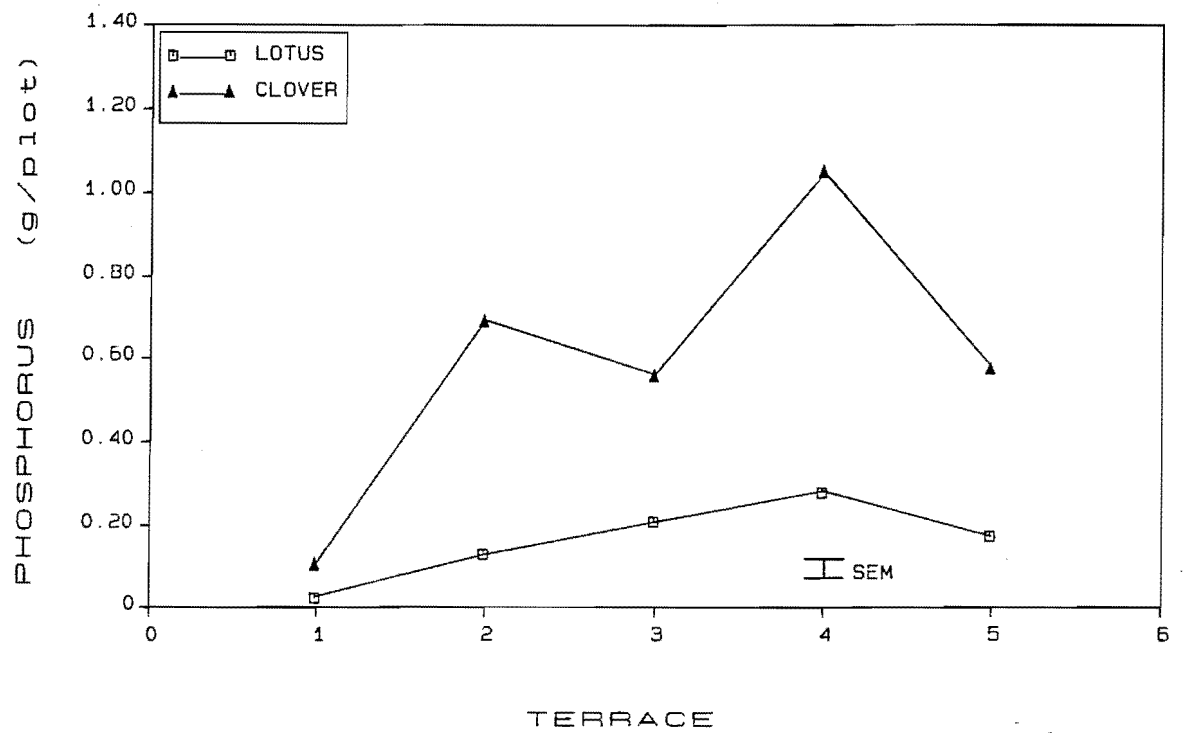


Figure 6.11 : Total shoot P uptake by lotus and clover on T1-T5 1982-1983

Table 6.10 : Legume Phosphate Efficiency with increasing P supply 1982-5 (DM g plot^{-1} per unit applied P (kg P ha^{-1})).

Season	Legume	P rate (kg P ha-1) 12.5	25	50	100	400	MEAN
1982-3	WC	4.3	4.0	4.9	7.2	2.5	4.6
	L	1.7	1.9	2.8	2.3	0.9	1.9
1983-4	WC	6.4	4.0	2.7	1.3	0.5	3.0
	L	7.8	7.6	6.0	3.6	1.5	5.3
1984-5	WC	2.8	1.4	0.7	0.3	0.05	1.1
	L	10.4	5.6	3.4	1.8	0.7	4.4
MEAN	WC	4.5	3.1	2.8	2.9	1.0	2.9
	L	6.6	5.0	4.1	2.6	1.0	3.9
SEM	WC	1.0	0.9	1.2	2.2	0.8	1.2
	L	2.6	1.7	1.0	0.5	0.2	1.2

Nitrogen tissue concentrations, only measured for the 1982-3 harvest, were higher in clover than lotus (25.1 vs 23.3 mg/g DM; $p < .004$). P rate did not significantly alter N concentrations. The only significant interaction, as for P concentration, was legume by terrace ($p < .001$). This was due to clover N concentrations increasing up to T4 then declining on T5 whereas lotus N concentrations were reasonably similar on all terraces (Fig. 6.12).

The pattern of total nitrogen uptake (Fig. 6.13) was almost identical to that of total P uptake, reflecting the dominant influence of herbage production rather than variation in tissue mineral levels.

6.4 DISCUSSION

6.4.1 Yield Estimation by Visual Score

Visual assessment gave good estimates of herbage dry matter yield, consistent with other Australasian studies (Campbell and Arnold 1983, Haydock and Shaw 1975, Smeaton and Winn 1981, Baars and Dyson 1981, Piggott and Morgan 1985, Piggot 1986). Correlation coefficients between estimated and actual yield for both legumes over two seasons (range r = 0.86 - 0.97) were better than those reported for North Island hill country pastures (range r = 0.60 - 0.90, Baars and Dyson 1981) and comparable with results from dairy pastures (r = 0.90 - 0.99; Piggott and Morgan 1985). They also compare very favourably with coefficients obtained from capacitance probe, weighted disk or height estimates (Piggott 1986). The close fit, can be attributed to careful field scoring and on-site checking, using quadrat grids as a portable standard reference for comparison (c.f. Haydock and Shaw 1975) and taking numerous small estimates

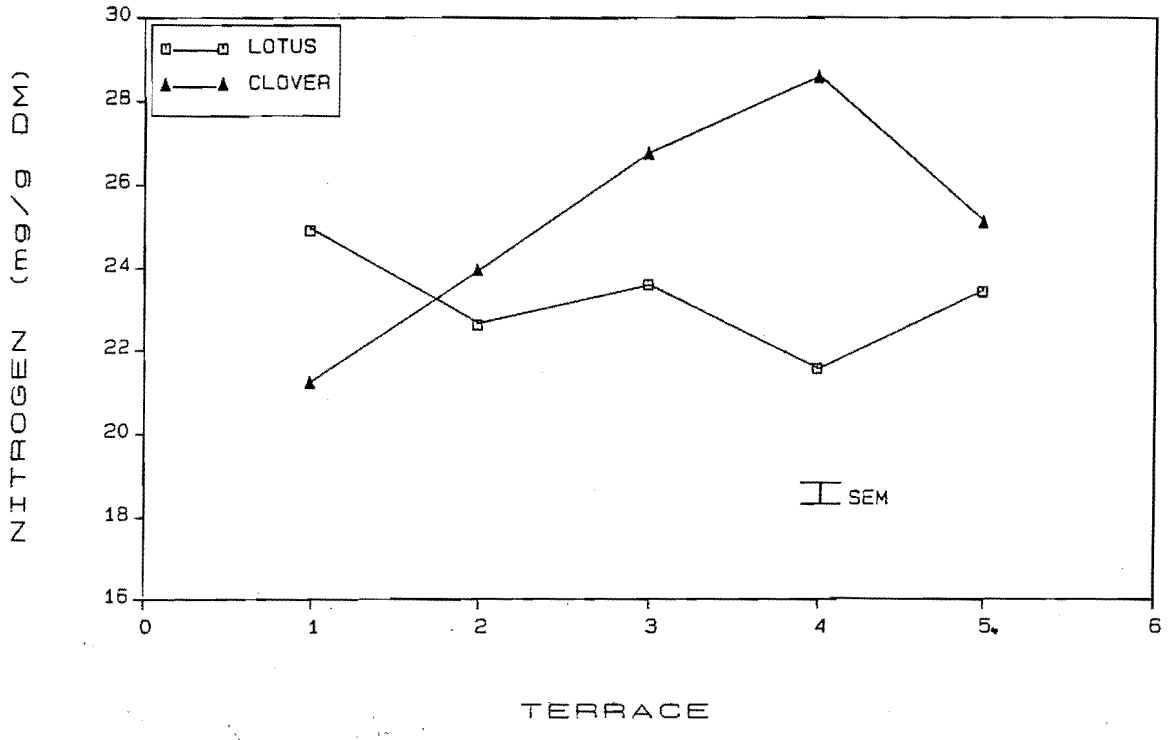


Figure 6.12 : Lotus and Clover shoot N concentrations on T1 - T5

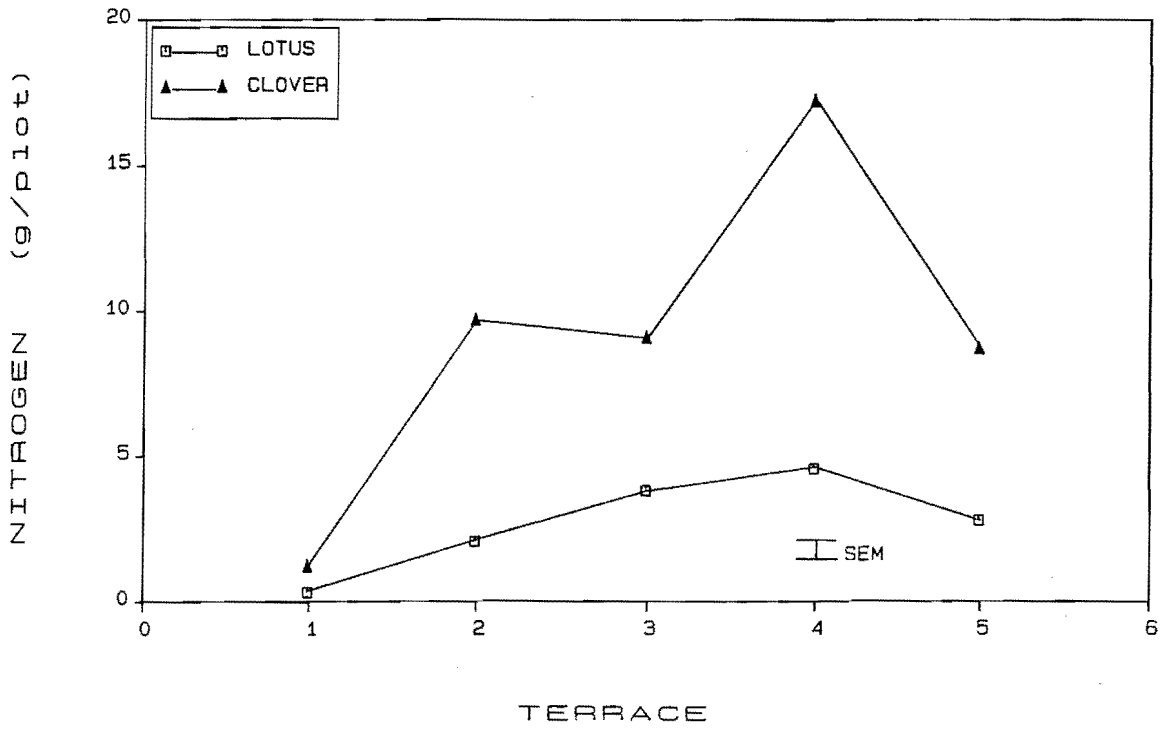


Figure 6.13 : Total shoot N uptake by lotus and clover on T1-T5 1982-1983

rather than a single whole plot estimate (c.f. Campbell and Arnold 1973, Baars and Dyson 1981). The most important source of error was probably associated with cutting the plots (Smeaton and Winn 1981).

6.4.2 Seedling Establishment

Visual scores 3 months after transplanting showed good establishment of both legumes over the first summer despite rainfall in January and February being about 75 to 48% below normal (Section 1.3). Transplant survival over the first summer (96% clover, 87% lotus) was similar to survival of summer transplants at Cave Stream (90% clover, 95% lotus; Kee 1981). The lower survival of lotus during summer at Puffers stream was due to the high mortality on T1. Subsequent winter survival was greater at Puffers Stream, (92% clover and 83% lotus vs 83% clover and 75% lotus at Craigieburn).

As applied P had no effect on survival on T1 and basal nutrients were not limiting, mortality was almost certainly not due to any explicit soil fertility factor. The most probable explanation is inadequate soil moisture. Obvious visual symptoms of moisture deficiency, curled leaves and wilting, were observed in both species on T1 during this period, particularly in lotus. The water holding capacity of T1 is low due to the coarse textured and free draining soil fabric (Chapter 1.4). Summer rainfall was below normal in 1981-2, solar radiation and windspeed were high (Chapter 1.3) and soil water deficits almost certainly occurred on T1. The greater sensitivity of lotus to moisture deficiency compared with clover, especially during establishment, is well known (Norris 1956, Levy 1970, Scott *et al.* 1974, Clifford 1975, Scott *et al.* 1976, Musgrave 1977a, Sheath *et al.* 1977, Sheath 1981).

The lower summer survival of clover at Cave Stream and the subsequent higher winter mortality of both legumes probably reflects the late planting date (22 December) and consequent failure to accumulate sufficient carbohydrate reserves. In addition there was greater exposure to frost lift at Cave Stream as there was more bare ground. Nevertheless survival at both valley terrace sites exceeded the 68-72% survival of transplanted lotus at 1460 m on warm north-west faces and 46-66% on shaded east-south-east slopes in the Grampian Mountains (Dunbar and Costello 1985).

As transplanting was deliberately chosen in this trial to minimise risk and maximise plant uniformity, factors affecting seedling establishment were comprehensively investigated in a synchronous study on T4 (Scheffel 1984).

Nodulation was excellent on seedlings prior to transplanting and visual examination of herbage after transplantation showed almost no evidence of inoculation failure. Nodulation was not investigated further because of the destructive sampling required, but did not appear to be a factor limiting establishment as reported with some oversowing experiments (Lowther 1980, Wedderburn and Lowther 1985). Furthermore soil pHs at Puffers Stream were all well above pH 4.7 suggested as the upper limit where lotus nodulation and establishment will improve with broadcast lime (Lowther 1983).

6.4.3 Herbage Production

6.4.3.1 Legume Production

The higher clover production in early spring (September 1982) was due to clover initiating growth earlier than lotus. Sheath (1981) demonstrated this effect in lowland pastures as did Kee (1981) in montane tussock grassland at Cave Stream. Clover maintained this advantage through the second growing season (1982-3) to out yield lotus. This also occurred in similar Canterbury sites (Davis 1981d, Kee 1981). Brock (1973) in a more favourable climate of Palmerston North, determined that full development of an efficient nitrogen fixing system took a year in lotus, much longer than clover. Furthermore, lotus channels photosynthetic assimilates into taproot and rhizome development resulting in lower initial aerial herbage production (Sheath 1981). Thus slower lotus establishment, possibly also influenced by a greater sensitivity to the low summer rainfall in the first season, is the most probable explanation for the lower lotus yield relative to clover. Slower lotus establishment from oversown seed is well known (Greenwood 1961, Armstrong 1974, Charlton 1977, Clifford 1975, Lowther 1980, Lowther and Littlejohn 1984).

Both legumes showed a strong response up to P50 within three months of transplanting (9 February 1982). P response pattern differed by the following spring (16 September 1982) with lotus showing the greatest response between P12.5 to P50 whereas clover responded over a greater range P12.5 to P100. The same pattern was apparent in DM yields at the end of the season (12 March 1983).

Lotus production peaked in the third season (1983-84) with the greatest rate of increase occurring as before, between P12.5 and P50 though yields were apparently still increasing at P400. In contrast, the incremental yield of clover between P12.5 and P100 was reduced from 1982-3 and there was no significant increase in yield beyond P25.

The most striking difference in performance occurred in the fourth season (1984-5). While lotus continued to respond to P as previously, albeit at lower total levels of production, there was a striking depression in clover yields at P levels greater than P25. Although the precise cause is unclear, the effect could be due to such factors as increased grass competition with the N enhancement after root and nodule degradation following harvests (Butler *et al.* 1959). Such an effect could be greater at the higher P rates as nitrogen accumulation in clover may increase with rate of applied P (Brock 1973). Alternatively, differences in rhizobia may be important. It has been suggested that lotus rhizobia are adapted to acid soils and are alkali producing in culture (Norris 1956, 1966, Brockwell *et al.* 1966) while those associated with *Trifolium* species are often acid producing in culture and adapted to neutral soils. Thus it is possible that symbiotic N fixation would tend to increase the rhizosphere pH of lotus and decrease it in clover. Haynes and Ludecke (1981b) have demonstrated that pH values of bulk soil from a pot trial were higher in soils where lotus was grown than those under clover. Possibly the rhizosphere pH was lowered sufficiently to mobilize phytotoxic levels of some elements, possibly aluminium or manganese.

There was no evidence of insect damage, either grass grub or porina, and it is unlikely, even if this were the case, that effects should be so consistent within high P replications and between terraces.

6.4.3.2 The Effect of Phosphate on Production

Edaphic effects were confounded by microclimatic differences between terraces. The lower terraces were more sheltered from the prevailing northerly winds and had lower mean wind velocities (Chapter 1.3). Plants on the northern edge of plots on the upper terraces were noticeably wind pruned, particularly the more upright lotus. Though microclimatic differences are probably small in relation to edaphic factors the experiment was repeated in uniform environmental conditions to directly investigate soil fertility (Chapter 8).

The differential herbage production on terraces appears to be due to three main factors: soil fabric, soil fertility and plant competition. The lower moisture holding capacity of T1, due to the open fabric and resulting summer soil moisture deficits, is probably the principal limiting factor on this surface.

The high correlation of clover DM in the absence of applied P with soil P fractions (Table 6.9) clearly indicates phosphate is a factor limiting production. The lower correlation of soil P with lotus (Table 6.9) suggests it can obtain adequate P for limited growth at lower P levels as has been previously found (Nordmeyer and Davis 1977, Caradus 1980, Kee 1981, Scott and Mills 1981). Its high correlation with pH is consistant with known responses to lime (e.g. Haynes and Ludecke 1981 and Lowther 1980). However, the limited number of terraces available for correlation of parameters, and the further limitation of only linear relationships being noted as significant, restricts interpretation of what are the actual causative factors and how they interact. Further study of seasonal nutrient pools and plant availability (McSweeny 1983) is required.

The reduction in yield of both legumes with increasing *Agrostis tenuis* (browntop) and *Anthoxanthum odoratum* (sweet vernal) cover is almost certainly due to direct competition. Meares (1975) and Metherell (1979) showed browntop competition reduced lotus and clover yields in pot trials. Resident grasses have also reduced field performance (Brock and Charlton 1978, Sheath 1981, Hall and Scott 1985).

The greater depressive effect of browntop and sweet vernal compared with *Festuca novae-zelandiae* or *Poa colensoi* indicates they are more aggressive competitors. Mouat and Walker (1958) showed browntop was a more aggressive competitor for P than either ryegrass (*Lolium perenne*) or cocksfoot (*Dactylis glomerata*). Browntop has also been demonstrated to reduce clover yield by accelerating soil moisture loss and consequently reducing P availability by increasing soil moisture tension (Jackman and Mouat 1970, 1972). They used an elegant soil solution culture experiment to show browntop to achieve near maximum growth at 3 ÌM P l^{-1} while clover required concentrations greater than 5 ÌM P l^{-1}. This difference helps explain the competitive superiority of browntop when both species grow in association under low P supply. A second experiment included lotus and showed it to be

intermediate between browntop and clover (Mouat 1983). Grasses have longer, finer root systems compared with legumes which gives them a greater ability to ramify through a given volume of soil and extract relatively immobile nutrients such as phosphorus (Evans 1977, Barrow 1975).

The lower regression coefficient of the lotus-resident grass equation (Fig. 6.7) relative to clover indicates it is less sensitive to competition. This is exactly what is expected from previous work. Haynes and Ludecke (1981b) demonstrated lotus had longer and finer root hairs compared with clover. Kee (1981) showed the greater productivity of lotus was associated with higher P recoveries than clover and the area exploited by roots for active P uptake was greater. He also showed in solution culture lotus roots were more efficient in P uptake over a range of concentrations, but particularly from very dilute solutions. Scott and Lowther (1983) found that competition in lotus/clover mixtures was for soil resources, not light, with lotus the more aggressive species. The major factor causing low clover yields was its inability to absorb P.

These results, all from low P levels or P deficient soils differ from competitive interaction on high fertility soils. Thus in the Manawatu Brock and Charlton (1978) found that lotus could not stand competition from clover and ingress of volunteer clover occurred in pure lotus stands. Greenwood and Sheath (1982) found in sub-humid Otago grasslands, where moisture was limiting, lotus regrowth after harvesting was slow and plants did not compete effectively with cocksfoot or volunteer white clover.

6.4.3.3 The Effect of Terrace on Production

The general form of the P response curves 1982-1985 (Figs. 6.3-6.5) is consistent with results obtained throughout the South Island high country though there are some significant local differences. Thus while lotus P response on an acid subsoil was very similar with maximum rate of response occurring between P12.5 and P50 and with little increase beyond P200, clover yield was depressed and showed only a small linear response from P25 to P400. (Davis 1981b, see also Davis 1981a). This sharply contrasts field trial results on a Pukaki terrace soil near Mt Possession, Ashburton, where clover continued to respond to P rates of 800 kg P ha^{-1} without reaching a plateau (Davis 1981d). The difference was attributed to aluminium toxicity (Davis 1981a, 1981b, 1981c).

The classic sigmoidal P response curves on Puffers Creek soils are further evidence for the well established P deficiency of Craigieburn and related soils (O'Connor 1967, Soil Bureau 1968, Sinclair and McIntosh 1983). More importantly the similar curvilinear P response by both legumes shows neither was grossly inhibited by any additional limiting factor as occurred in Davis's subsoil experiments.

Precise comparison of actual response rates between different trials is confounded by different establishment techniques, basal and treatment fertiliser levels, climatic differences, growth period and time of harvesting. For instance while clover response at Mt Possession at P100 (Davis 1981d) was only 42% of the maximum yield compared with

72% with P100 at Puffers Stream it is not clear if the continued response at higher P rates at Mt Possession was due to direct drilling, fertiliser placement, shorter trial period, the particular growing season, or interaction with other unknown factors. Clover response curves at Mesopotamia, Rangitata Valley, 28 months after sowing (Kee 1981) were almost identical in form to hose of Puffers stream 29 months after transplanting. Lotus production at Mesopotamia only increased 1.4 times between P25 and P100 (Kee 1981) compared with 2.3 times over the same range at Puffers Stream.

Noting the above reservations, legume performance in trials at the Cave and Puffers Stream sites can be compared. Transplant techniques and basal fertilisers were identical (Kee 1981). Pyrophosphate, (used as the P source at Puffers Stream) has been shown to be equally effective as orthophosphate (used as the P source at Cave Stream) in supplying P to phosphate deficient wheat, maize and barley (Gilliam 1970, Surgucheva *et al.* 1974). Roots can readily absorb pyrophosphate directly and it is also rapidly hydrolized to orthophosphate by root phosphatases (Sutton and Larsen 1964, Raweiny *et al.* 1976). Two P treatments 25 and 50 kg P ha^{-1}, were common to both trials and two differed slightly, 12.5 and 150 kg ha^{-1} at Cave Stream compared with 10 and 100 kg ha^{-1} at Puffers Stream. However P response curves (Fig. 6.5) show the difference between these rates is not great so the discrepancy is likely to be small.

Climatic differences were not great between the two trial periods and would probably favour production at Cave stream where the trial site is more sheltered. Precipitation during the main period of the trial, 1979 to 1980, was 14% and 15% above normal at Craigieburn Forest (N.Z. Meteorological Service 1979, 1980) but was only slightly below normal for the period of the Puffers Stream trial (Chapter 1.4).

It is significant herbage production differed between the two sites though legume response patterns were reasonably similar (Fig. 6.8). Clover yield at the end of the first growing season (16.5 month after establishment) at Puffers Stream was considerably higher than at Cave Stream (12 months). Lotus yields were similar at both sites. By the second season clover yields had dropped to the same level at both sites while lotus production increased at both sites but was 1.5 times greater at Puffers Stream. Production was not measured in the third season at Cave Stream but may have dropped, as occurred at Puffers Stream.

The greater legume production at Puffers Stream in both seasons after establishment could result from superior establishment with spring planting rather than summer planting at Cave Stream. For instance, with oversown legumes Scott *et al.* (1976) showed a 2-3 fold decrease in establishment from early to late spring sowing.

Alternatively, results may be explained by properties of the more strongly leached soil at Cave Stream. The upper profile at Cave Stream (0-30 cm; C3 Tonkin 1981) is more acid than at Puffers Stream (T_4; Harrison and Swift 1985); pH (KCl) ranges from 4.2-4.4 vs 4.5-4.8. Topsoil (0-10 cm) levels of exchangeable aluminium are higher (2.3 vs 0.6 meq/100 g), with lower levels of Ca Mg K Na, lower inorganic P levels (33-27 vs 39-32 mg/100g) and higher P retention levels (67-93% vs 44-64%). As

nitrogen levels were higher at Cave Stream (0.26-0.57% vs 0.13-0.32%) and adequate levels of basal cations and sulphur were applied in both trials, it is unlikely these are the principal factors determining the difference in yields. Conversely many studies have shown soil acidity to be a major factor in determining the relative performance of the two legumes (During *et al.* 1964, Lambert *et al.* 1974, Nordmeyer and Davis 1977, Lowther 1977, 1980, Morton 1981, Haynes and Ludecke 1981a, 1981b, Davis 1981a, 1981b, 1981c, Scott and Mills 1981, Lowther 1983, McIntosh *et al.* 1984, Floate *et al.* 1985).

Exchangeable Al levels in the Cave Stream topsoil are similar with those causing Al toxicity in white clover in pot experiments (Haynes and Ludecke 1981a,b, Davis 1981a,b,c). Therefore it is a reasonable supposition that Al levels in the topsoil were responsible, at least in part, for the lower clover response at Cave Stream relative to Puffers Creek. Reduced availability of applied P due to the higher retention of P on colloids may equally be a concomitant contributing factor. Both of these explanations are consistent with the similar lotus yields in the first season between sites, as lotus is more tolerant of soil acidity (see above references) and more effective in extracting low levels of soil P at lower pH (Brock 1973, Kee 1981, Davis 1981a, 1981b, 1981c, Haynes and Ludecke 1981b).

6.4.4 Herbage Mineral Content

The higher tissue concentration of N and P in clover shoots compared with lotus (Figs. 6.9, 6.10) agrees with numerous field and pot trials (Davis 1974, Scott *et al.* 1974, Crush 1974, Nordmeyer and Davis 1977, Metherell 1979, Hart *et al.* 1980, Lowther 1980, Scott and Lowther 1981, Haynes and Ludecke 1981b, Davis 1981a, 1981b, Hart *et al.* 1981b, Hart and Jessop 1983) but contrast with results obtained by Brock (1973) and Lucas *et al.* (1981). Actual levels are difficult to compare directly due to differences in applied fertilisers and seasonal variations but the concentration range of P (0.10 - .20% DM for lotus and 0.14 - .23% for clover) is within the lower range of values reported for the species by other workers on similar soils, Scott *et al.* (1974) (0.26-0.29%, 0.26-0.30%), Lucas *et al.* (1981) (0.19 - 0.25%; 0.14 - 0.22%), Davis (1981b) (0.19 - 0.27%; .25 - .64%) Davis (1981c) (0.15 - 0.27%; 0.25 - 0.27%), Haynes and Ludecke (1981c) (0.14 - 0.49%; 0.12-0.56%), Hall and Scott (1985) (0.18 - .26%; 0.18 - 0.44%). The lower levels in this study are probably due to the autumn harvest where more old tissue with lower P levels is present (Hart and Jessop 1983).

The increase in shoot P concentrations in lotus above P_{50} (Fig. 6.10) while DM only slightly increased (Fig. 6.5a) is strongly indicative of P storage. This was most probably stored as inorganic P rather than lipid, ester or nucleic acid P (Hart and Jessop 1983). Storage probably occurred in vacuoles (Bielski 1973). A similar increase in tissue P when growth response to supplementary P supply has been observed in tomatoes, soybean, barley and white clover (Houge *et al.* 1970, Lee *et al.* 1976, Chapin and Bielski 1982, Hart and Jessop 1983). This sequestering of P may be an important factor influencing the increased DM yield in the following season (Fig. 6.5b). This result, and

the continued increase of both shoot P and DM with increasing P application in clover, is the reverse of what occurred in solution culture (Hart and Jessop 1983).

The P ecology of white clover was typical of ruderal species adapted to fertile soils. Clover showed a marked response to improvements in P supply by increasing both shoot concentration and DM, characteristic of a ruderal plant, but its growth at low P levels is poor. Plants adapted to low P availability are characterized by low growth rate, small responses to improvements in P supply and often maintain high tissue nutrient concentrations as a buffer against future nutrient shortage (Chapin 1980). Lotus, with its ability to respond to low rates of P but limited response at higher P rates (Fig. 6.5a) while sequestering tissue P at high supply thus has strong affinities with low P adapted plants. However its behaviour the following season (Fig. 6.5b), where unfortunately no nutrient data are available, is more analagous to a ruderal plant.

Shoot tissue concentrations in both legumes are grossly deficient according to critical concentrations suggested by McNaught (1970) and Kee (1981). McNaught proposed a tentative critical P concentration for white clover between 0.30 - 0.40 % P and Kee estimated the critical concentration for lotus ranged between 0.25 - 0.30% P. The decreasing rate of DM response to increasing P rates in both species (Fig. 6.5) strongly suggest these critical concentrations are too high.

Phosphorus efficiency, using the simple criterion of DM per unit applied P (Blair and Cordero 1978), varied depending on time lapsed since application (Table 6.10). In the second season after establishment, when applied P was presumably still readily available, both legumes showed the greatest P efficiency at high P rates. The higher P rate at which this occurred for clover P100 relative to lotus P_{50} (and P12.5 in 1983-4) is consistent with their ecological adaptation as discussed above. When lotus produced its maximum DM yields, in the third (1983-4) season, it was, on average, more P efficient across the range of applied P than clover in the preceding season.

The superior P efficiency of lotus at low P rates, is demonstrated when soil P levels would have been, at their lowest in the fourth season due to depletion of the initial applied P through harvest removal, leaching losses and adsorbtion on soil colloids. This also explains why P efficiency dropped for both legumes with increasing time lapse from initial P application. These results are in excellent agreement with previous work (Brock 1973, Nordmeyer and Davis 1977, Hart *et al.* 1981b, Kee 1981, Scott and Mills 1981, Hart and Jessop 1981a 1983).

What is responsible for the highly significant tissue nitrogen concentration terrace by legume interaction is unclear. Stepwise linear regression analysis against 30 soil chemical parameters (Harrison and Swift 1985) produced few significant relationships and none that were readily interpretable. For example in the upper 10 cm, no parameter was significantly correlated with clover N concentration and with lotus, a negative relationship with CEC was just significant ($p < .04$). In the next horizon (10-20 cm) clover N was negatively correlated with exchangeable magnesium ($p < .03$) and lotus again with CEC though not significantly ($p < .14$).

Legume N concentrations were, however, significantly related to total DM production:

Clover N conc.	= 20.691 + 0.013 DM		(r = 0.875)
Lotus N conc.	= 24.800 - 0.130 DM		(r = 0.838)

Gibson *et al.* (1956) have shown that N fixation increases with total DM production particularly where P is in excess supply; this may partially explain the clover results. Hart *et al.* 1981a showed clover nodules to be more efficient than lotus in accumulating N which may explain the higher clover N content. The high lotus N content on T1 is almost certainly due to limitation of DM growth (mean DM/plot only 2.5 g) where soil N was readily available and hence accumulated.

Unlike P there is no consistent trend for the difference in N content. This probably reflects the greater variability in N supply through site and experimental effects on nodulation and N fixation. It is noteworthy that tissue N concentrations (clover 2.1 - 2.8%; lotus 2.1 - 2.5%) are within the range of reported values (e.g. Brock 1973, Lucas *et al.* 1981, Davis 1981c) but lower than values McNaught (1970) suggested as critical percentages for clover - in the range 4.5 - 5.5% N. Clover, by this criterion, was grossly N deficient. Kee (1981) also found clover N concentrations to be far below the suggested critical range during the four years of a trial at Mesopotamia. In view of the clearly established increase in N fixation with increased levels of P (Gibson *et al.* 1975, Nordmeyer and Davis 1977) it is debatable whether McNaught's N concentrations were in fact limiting. Hart *et al.* (1981a), however, have shown lotus and clover directly supplied nitrate, at high P levels outyielded nodulated plants. They attributed this result to N limitation : the nodulated legumes were apparently unable to fix sufficient N to give similar yields to NO_3 supplied plants.

6.5 CONCLUSION

On moderately acidic high country yellow brown earth soils lotus established more slowly than clover. Clover herbage yield and dry matter production per unit P applied were greater than lotus the first season after establishment. Lotus yields and P efficiency in herbage production were greater than clover in the second and third seasons after establishment. In the third season clover yields at the highest P rates were less than control plots without applied P.

Three main factors influenced legume yield: soil fabric, soil fertility and plant competition. Soil fabric, determining soil water holding capacity, was a major factor effecting seedling establishment and subsequent development. Lotus was more sensitive to summer soil water deficit than clover though neither legume is suited to soils with limited water holding capacity.

All soils were P deficient with both legumes strongly responding to applied P. Lotus response was proportionately greater than clover at low rates of P. Without added P soil

soil acidity and P status were the topsoil chemical variables most strongly correlated with lotus and clover production. Legume yields were lower on more strongly leached soils and this is tentatively ascribed to increased soil P competition for applied P and possibly direct effects of aluminium.

Herbage yields were inversely related to abundance of resident grasses. Clover yields were reduced proportionately more than lotus. Direct competition was almost certainly responsible.

These results do not disprove the working hypothesis. It is concluded the ecological response patterns of clover are typical of a ruderal species while lotus has affinities with both ruderal and low fertility adapted plants. Clover is the legume suited for intensively managed pasture with high fertiliser input. Lotus is clearly superior for low P situations where P efficient herbage production and persistance is required. These conclusions apply to high country soils where soil water deficits are not limiting and grazing management is suitable.

CHAPTER 7 PHOSPHATE RESPONSE OF *LOTUS PEDUNCULATUS* AND *TRIFOLIUM REPENS* ON SIEVED AND INTACT HIGH COUNTRY YELLOW BROWN EARTH SOILS.

7.1 INTRODUCTION

Glasshouse pot experiments reduce the ecological variability encountered in field trials and allow investigation of single factor, or multiple factor interactions, under controlled conditions. To directly compare edaphic factors in this study it was necessary to eliminate effects of climatic differences between sites 15 km apart and micro-climatic differences between members of a terrace sequence (Chapter 1). So the principal field experiment (Chapter 7) was repeated in a glasshouse (Chapter 9).

Unfortunately glasshouse conditions themselves can have an appreciable effect on plant dry matter yield and nutrient uptake (Milikan 1961, Stefanson & Collis-George 1974a,b, Ross *et al.* 1978, Caradus & Snaydon 1986). Large undisturbed soil cores from the main surface of both sites were compared with soil prepared using standard pot trial procedures to test the following hypothesis:

> *Standard pot trial soil preparation techniques do not significantly affect legume herbage response to edaphic factors on either Cragieburn or Puffers Creek high country yellow brown earth soils.*

7.2 MATERIALS & METHODS

7.2.1 Experimental Design

The experimental design was a completely randomised 2x2 factorial with soil type and structural preparation as treatments. Treatments were replicated five times. The sixth intact Craigieburn core was retained in the glasshouse and used for trial root extraction prior to main harvests. The specific treatments were:-

(A) Soil : Puffers Stream T4 & Cave Stream C4;
(B) Structure : Intact Field Cores & Reconstituted Cores.

7.2.2 Soils

Six intact soil cores from Craigieburn cutting and five from Puffers Stream were extracted on the 28 - 29th April 1983 using 48cm diameter by 30cm steel cylinders. At Craigieburn, the cores were sampled from a 20m by 30m area, 10m from the northern scarp of the surface (Grid Reference : NZMS1 S66 215 041). The Puffers Stream cores were systematically sampled on the southern circumference of a 50m circle centred on the experimental plot on the main terrace surface T4 (Grid Reference : S66 344 022). Cylinders were subjectively positioned in *Festuca novae-zelandiae* grassland to avoid tussocks and shrubs and carefully extracted containing undisturbed cores.

Vegetation adjacent to cores was carefully removed and mineral soil was incrementally depth sampled within horizons as follows :-

Craigieburn		Puffers Stream	
Ah	1-15cm	Ah	1-12cm
Ah/Bw	15-18cm	Bw	12-16cm
Bw	18-25cm	Bw	22-25cm

In addition, four 15cm x 15cm cores per site were taken to measure top and subsoil bulk densities.

Soils and cores were transported to a Lincoln College glasshouse sterilised a week previously with 3% formalin and stored overnight. The glasshouse was heated in Winter and ventilated by a thermostatically controlled fan and louvers in Summer. A thermohygrograph, positioned in the centre of the glasshouse, continuously recorded air temperature and relative humidity during the experiment.

Intact cores were carefully trimmed to a uniform depth of 25cm, seated in galvanised iron trays, and watered. Soil horizons were bulked, crumbed and mixed, coarse roots and stones removed, thinly spread on trestles and air dried for a week. When dry, horizons were passed through a 4mm sieve removing fine roots and stones.

Artificially reconstituted cores, hereafter termed sieved cores, were reconstructed in identical cylinders to the intact cores. The weight of air dry soil required to give the same bulk density per horizon in undisturbed soil was calculated using the bulk densities from the 15cm cores. Each horizon was then set in cylinders in the same order as the original field horizon.

Cylinders, painted grey to minimise soil heating, were placed in 40cm deep trays on trestles 100cm x 90cm apart (Plate 7.1). Glasshouse position was determined by random number.

Species composition and percentage cover was recorded on intact cores before spraying with systemic herbicide (1% Roundup, active ingredient Glyphosate) on the 3rd May. All cylinders were re-sprayed with glyphosate on the 4th June. Surface vegetation was dead by the 11th June and was removed by scalpel with minimal disturbance of surface structure. Any large roots eg. *Coprosma*, were cut 1cm below the surface and left in situ. Exposed surface stones were also removed. Surface compaction was measured using an ELE penetrometer, taking 3 readings per core.

Basal fertilisers were surface applied in solution by 20ml pipette þ 0.1ml or bulked with sand, by hand, on the 15th - 16th July as follows :-

Compound (Analar grade)	Form	Elemental Rate (Kg/ha)			
Potassium dihydrogen phosphate	KH_2PO_4	K	31.5	P	25.0
Potassium sulphate	K_2SO_4	K	100.0	S	41.0
Magnesium sulphate	$MgSO_4$	Mg	100.0	S	131.7
Calcium sulphate	$CaSO_4\ 2H_2O$	Ca	25.0	S	20.0
Sodium molybdate	$NaMoO_4\ 2H_2O$	Mo	0.4		

Nitrogen, at a rate of 120 Kg/N/ha^{-1}, was surface applied as urea immediately after the first harvest (1 October 1982). The urea was dissolved in deionised water and applied by 100ml pippette þ 0.1ml).

Lotus pedunculatus cv 'Maku' was sown on the 2nd July at a rate of 320 seeds per core, giving approximately one seed 6.5 cm^2. Seeds were inoculated at standard rates with lotus specific rhizobia ('Nodulaid') immediately prior to sowing. All cores were sprayed with a fungicide mixture of 0.14% Captan (active ingredient 50% captan) and 0.05% Benlate (A.I. 50% Benomyl) as a precaution to control possible root pathogens on the 6th July, and again on the 24th August. Three weeks after the third harvest (24th February, 1983) insecticide (vapona 1% v:v solution) was sprayed on all cores to control onion thrip (*Thrips tabacci*) which were increasing on some cores.

Cores were lightly surface watered after seeding and then regularly bottom watered 2-3 times weekly with deionised water for the duration of the experiment. Cores were kept weed free.

Herbage was harvested four times, harvesting commencing at the onset of flowering, except for the fourth harvest, as follows :-

Cut	Date	Year	Day	Harvest	
1	27-29th October	1982	118	Tops	1/2 Roots
2	13th December	1982	163	Tops	
3	4th February	1983	216	Tops	
4	12th September	1983	408	Tops	1/2 Roots

The insecticide caused variable degrees of tissue damage so herbage was removed on all cores to ensure uniformity 4 weeks after the 3rd cut (26th Febrary).

Aerial herbage was cut to within 1cm of crowns, dried for 48hrs at 70-72 C and weighed þ 0.01g. Oven dried samples were cut into 2-3cm lengths, mixed and quartered (Allen, 1974), ground in a hammer mill to pass through a 1mm sieve and stored in plastic vials for chemical analysis.

The number of live plants (crowns plus seedlings) were counted at the first harvest. Cores were then halved with equal numbers of plants in each half. One half was randomly

chosen for root extraction and the other left for regrowth. A metal plate was inserted after removing the half core and the void filled with surplus Craigieburn topsoil.

The half core was accurately cut into four sections :

A	0- 5 cm	depth
B	5-10 cm	"
C	10-15 cm	"
D	15-25 cm	"

The outer 3cm circumference of each section was separated to isolate edge effects. Bulk density was measured by inserting a 5.4cm x 5cm cylinder into each inner section, trimming to volume, oven drying for 24hrs at 102 C and weighing þ 0.01g. Roots and small stones were extracted from the bulk density sample and weighed.

Roots and stones were extracted from inner and outer sections by gentle hosing over a 0.5mm mesh sieve, then washed for 30 minutes in a 0.25mm mesh rotary sieve pressure spray system. Roots and detatched nodules were then separated from fine gravel by washing and flotation in the laboratory. Complete seperation of resident dead roots from live lotus roots was not feasable. Dead roots were separated from lotus roots as far as possible, before the percentage of live roots was visually scored. Fifteen samples were randomly chosen for complete fractionation to check visual scoring. All roots were oven dried for 48hrs at 70 °C and weighed þ 0.01g. Stones and gravel were dried for 24hrs at 80 °C and weighed þ 0.01g.

Root distribution at the final harvest was determined by extracting five 2.5cm x 25cm core samples per soil core and bulking them into 0-4cm, 4-8cm, 8-12cm, 12-18cm and 18-25cm depth increments. Roots were then extracted and dried as before. The remainder of the roots were washed free of soil over a 1mm sieve, stones retained, and treated as previously.

Aerial herbage at the final harvest was cut 5cm above crown level for nutrient analysis, then the remaining stones and runners cut to within 1cm of the crown. Many runners were restricted by and accumulated around, the cylinder walls. These were harvested separately. Runners in a similar position, but below ground level, were recorded as a separate fration termed rhizomes. Roots were gently hosed free of soil over a 1mm mesh sieve, stones and gravel collected, and treated as previously.

7.3 RESULTS

7.3.1 Resident Vegetation

Inter tussock species composition and cover differed between the two sites (Table 7. 1).

Table 7.1 Species cover on Cragieburn & Puffers Stream Intact Soil Cores

Species	% Cover per Core					
(a) Craigieburn Cutting	1	2	3	4	5	Mean
Agrostis/Anthoxanthum	50	60	80	70	50	62
Moss	20	20	10	+	10	12
Poa colensoi	10	5		10	30	11
Lycopodium fastigiatum	10	5		10	5	6
Coprosma petrei			10			2
Gaultheria depressa				10		2
Luzula rufa		2	3			1
Hieracium " praealtum "	5	7				2
Hieracium " pilosella "					+	
Brachyglottis bellidioides					+	
(b) Puffers Stream	1	2	3	4	5	Mean
Raoulia subsericea	15	5	80	45	50	39
Coprosma petrei	45	80			30	31
Poa colensoi	15	10	10	35	15	17
Agrostis/Anthoxanthum	15	5	+	10		6
Moss	5		5			2
Discaria toumatou	2		2			1
Hieracium " pilosella "	+			5		1
Pimelia oreophilla				5	+	1
Gentiana corymbifera	+	+	+	+	+	
Senecio bellidioides	+	+	+			
Leucopogon frazerii	+		+			
Celmisia gracilenta		+			+	
Luzula rufa					+	

7.3.2 Plant Establishment

Plant establishment 46 days after sowing (cut 1) was 1.3 times higher on sieved soils compared with intact ($p<0.001$, Table 7.2). The differences between soils and the soil x structure interaction were not significant.

Table 7.2 Number of Live Plants 46 Days after Sowing

Soil	Structure Intact	Sieved	Mean	SEM
Craigieburn	134	170	**152**	6.0
Puffers Stream	124	171	**147**	
Mean	**129**	**170**		**6.0**

7.3.3 Soil Stone Content and Bulk Density

Total stone and gravel weight per core, summed from both half core fractionations, was nearly nine times greater in Puffers Stream than Craigieburn soils, principally in intact cores ($p<0.02$, Table 7.3)

Table 7.3 Total Core Stone Content > 1mm (g)

Soil	Structure Intact	Sieved	Mean	SEM
Craigieburn	420	291	**356**	786
Puffers Stream	5652	692	**3172**	
Mean	**3036**	**492**		1111

Stone distributions in the half core fractionated showed a significant soil by structure interaction ($p<0.02$, Fig. 7.1) The accumulation of surface stones on intact Puffers Stream cores (depth 0cm) and in the upper topsoil (0-5cm) is striking, even allowing for the influence of a small boulder in one core topsoil weighing 4.6 times the average stone weight of the other four replicates. Stone content increased significantly with depth ($p< 0.008$).

Bulk densities in intact cores were always greater than in sieved cores ($p<0.001$, Fig. 7.2). Puffers Stream densities similarly always exceeded corresponding Craigieburn densities ($p<0.001$). Bulk densities increased significantly with depth in both soils ($p<0.001$). The sharp rise in the intact Craigieburn Ah density (5-10cm depth) reflects the influence of one core 1.1 times the average of the remainder (0.91 vs 0.81 g/cm3) and may be anomalous. The rise in the intact Puffers Stream Ah/Bw horizon (10-15cm depth) is due to stones. Stone free bulk density was only 0.99g/cm3, compared with 1.06 g/cm3. Stone removal only affected bulk density in one other horizon, the intact Puffers Stream Ah (0-5cm) : densities fell from 0.89 to 0.76 g/cm3. The soil by structure interaction was not significant.

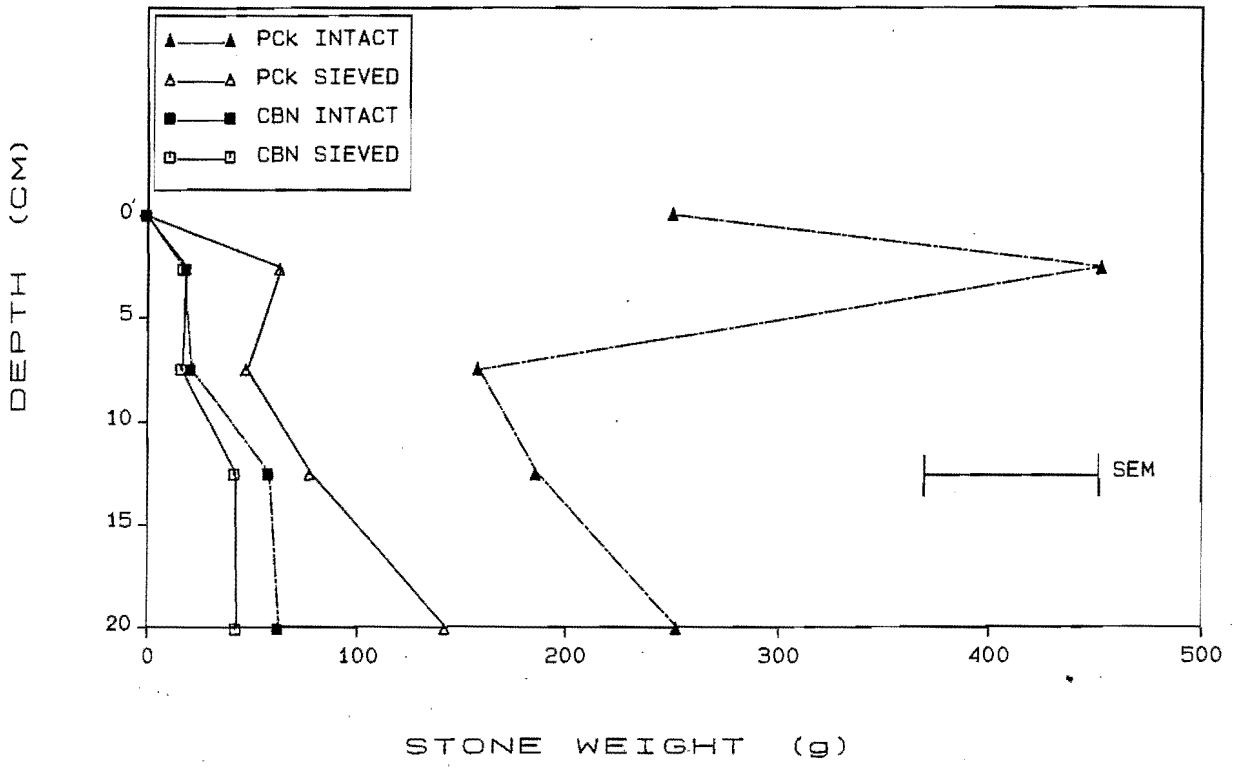


Figure 7.1 : Stone distribution in sieved and intact Puffers Stream and Craigieburn soil cores.

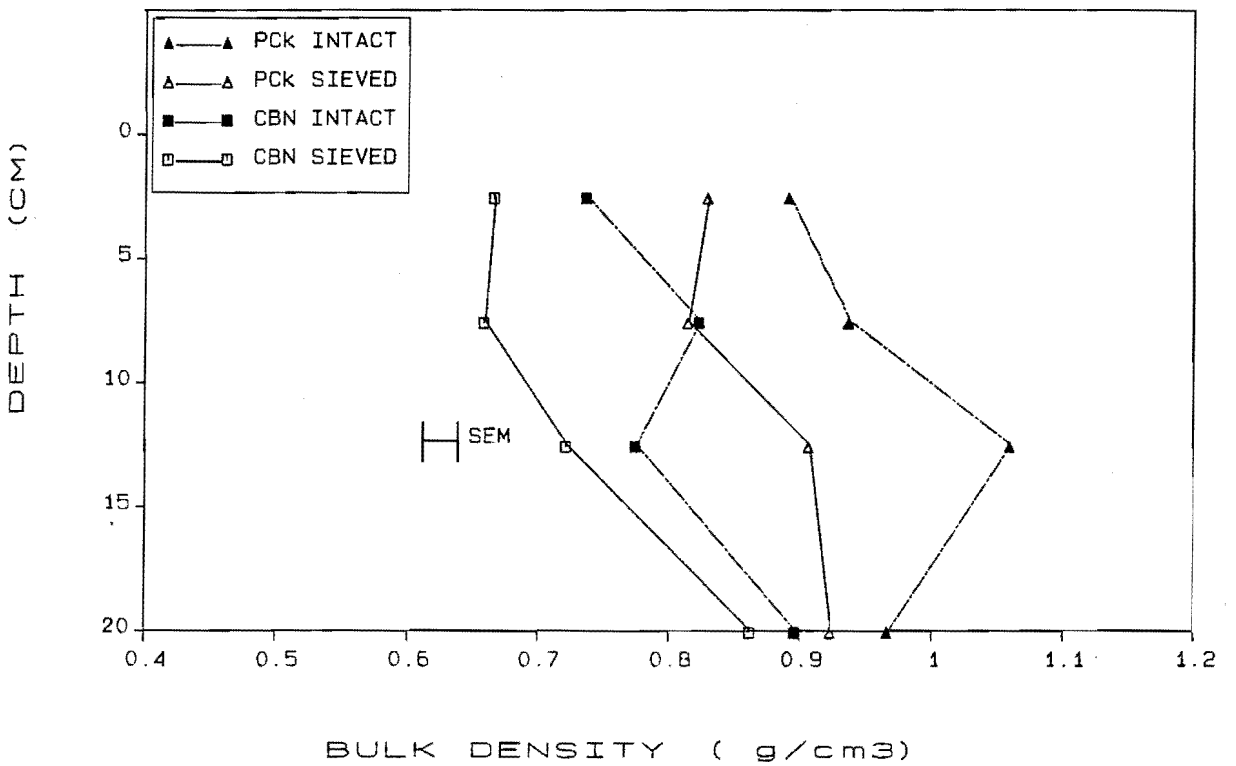


Figure 7.2 : Bulk density depth change in sieved and intact Puffers Stream and Craigieburn soil cores.

Surface compaction, as expected, was greater in the intact cores ($p<0.001$). The soil by structure interaction was highly significant ($p<0.01$). Penetrometer resistance is shown in table 7.4.

Table 7.4 Penetromiter resistance on sieved and intact soil ($kg/cm^{2)}$

Soil	Structure		Mean	SEM
	Intact	Sieved		
Craigieburn	0.69	0.44	**0.66**	0.02
Puffers Stream	1.19	0.51	**0.82**	
Mean	**0.94**	**0.47**		0.02

7.3.3 Herbage Yield

Sieved cores produced 1.7 times the dry matter from intact cores at the first cut ($p<0.001$; Plate 7.1) and Puffers Stream 1.2 times the yeild of Craigieburn soil ($p<0.007$). The differences in production between intact and sieved Craigieburn soils was 2.6 times greater than with Puffers Stream soils and resulted in a highly significant soil x structure interaction ($p<0.01$, Fig. 7.3).

Nitrogen application immediately after the first harvest dramatically affected yields. The second cut, 56 days later, showed no significant differences between treatments (Fig. 7.3). After a further 74 days (cut 3), production was 1.4 times greater on Puffers Stream soils ($p<0.001$), the only significant difference.

By the final harvest, six months later the following Spring, production was 1.6 times higher on the sieved cores ($p<0.001$). Other differences were not significant (Fig. 7.3).

7.3.4 Root Yield

Estimated lotus root weights, calculated from visual scores of the percentage composition in the total root sample, were very close to the true root weights :

Lotus Root Weight = 9.5 + 1.07 Est. Root Wt. ($r=0.921$).

Estimated weights were used in all statistical analyses of the first cut root data.

Root weights were always greater, per horizon, in intact soils ($p<0.001$). Roots decreased with depth in all treatments ($p>0.001$), but distribution patterns differed between soils and structure treatments ($p<0.001$, Fig. 7.4). This soil by structure by depth interaction was due to Craigieburn intact subsoil root weights remaining similar between 10cm to 25cm, whereas Puffers Stream roots decreased by a factor of 2.7 over the same depth. Second order interactions, soil by depth and structure by depth, were not significant. Effects due to container constriction were minimal. Analysis of variance results were identical when the unrestricted root data (i.e. including the outer circumference) were analysed.

Plate 7.1 Lotus herbage production on sieved and intact Craigieburn soil

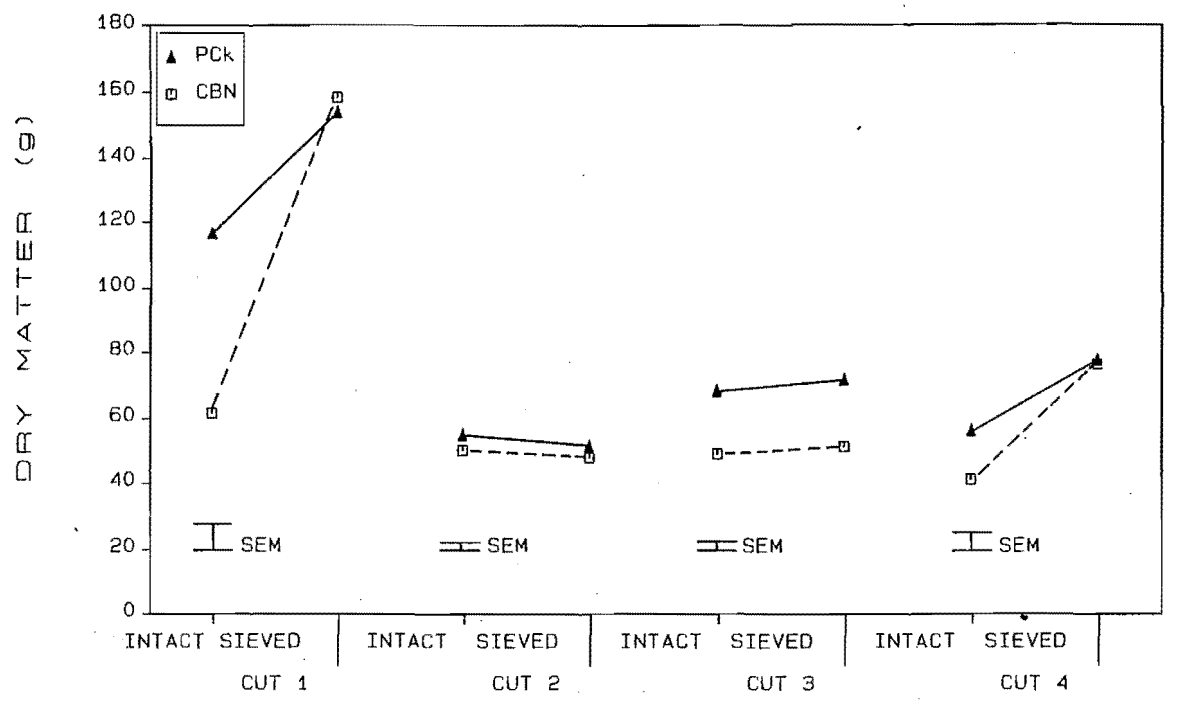


Figure 7.3 : Herbage yield on.sieved and intact Puffers Stream and Craigieburn soil cores, 1982-1983

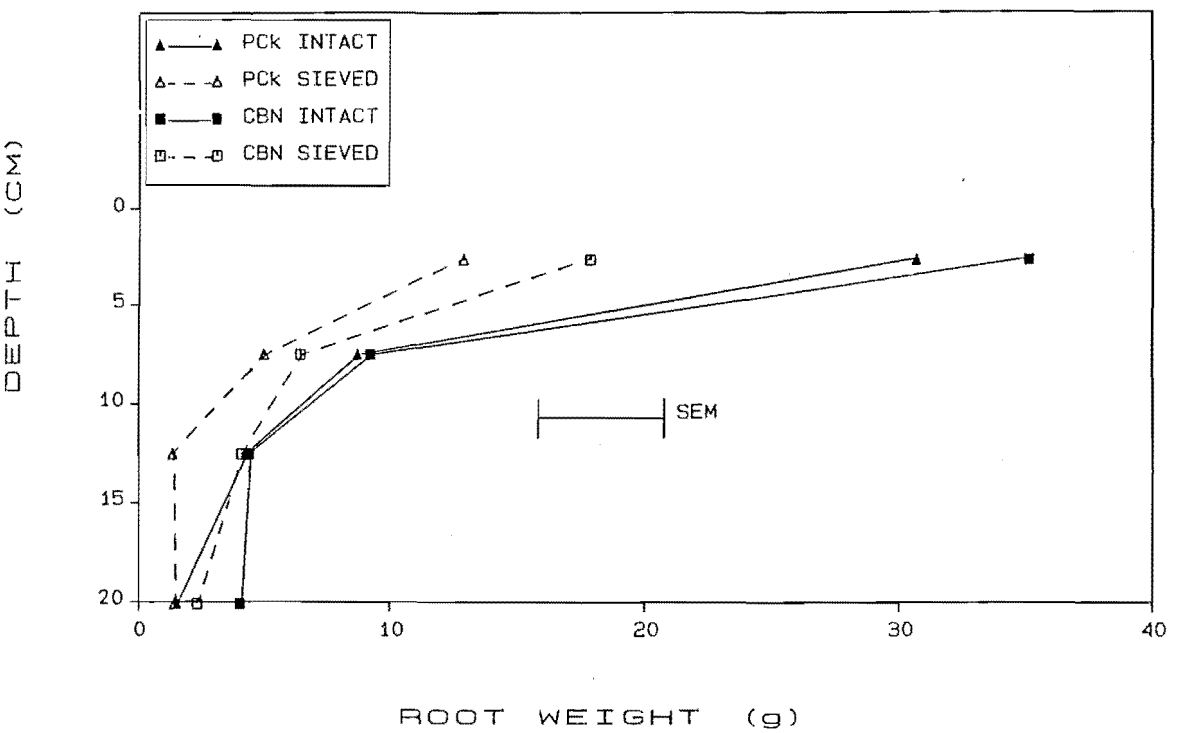


Figure 7.4 : Root DM distribution by depth in sieved and intact Puffers Stream and Craigieburn soil cores, cut 1.

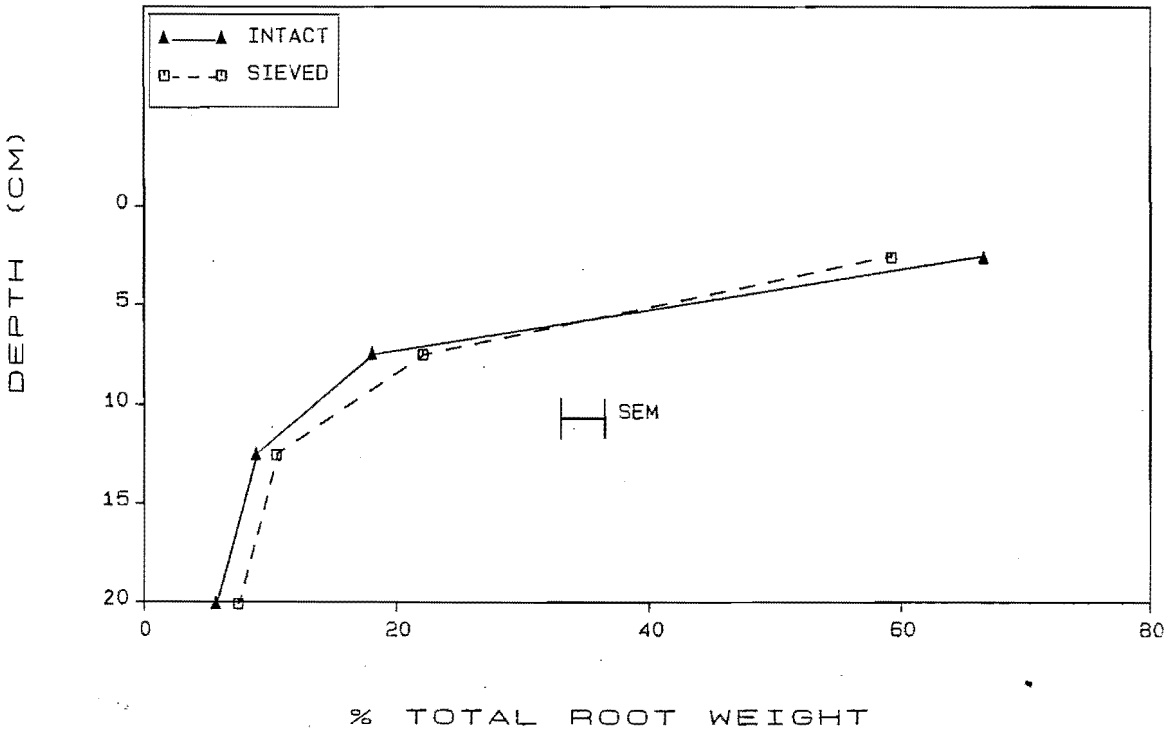


Figure 7.5 : Percentage of total root DM occurring at varying depth in intact and sieved soil cores, cut1.

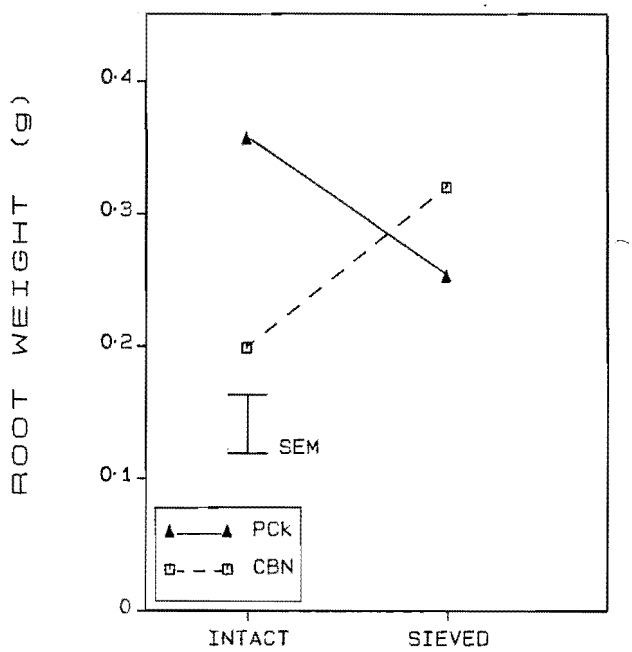


Figure 7.6 : Root DM yield on sieved and intact Puffers Stream and Craigieburn cores, cut4

Percentage total root weights were plotted to directly compare root distribution patterns in sieved and intact cores (Fig. 7.5). Proportionately more roots occurred in the upper Ah horizon (0-5cm) of intact cores and proportionately less in the remaining horizons.

Nine months later (Cut 4) Craigieburn root weights increased 1.6 times between intact and sieved cores sharply contrasting the 1.4 times decrease between similar Puffers Stream cores giving a highly significant interaction ($p<0.01$, Fig. 7.6). Root weight decreased with depth ($p<0.001$) but percentage root weights did not differ between soils or structure treatments (Fig. 7.7).

7.3.5 Herbage Mineral Content

Herbage phosphorus concentration showed a highly significant interaction between soil and structure treatment at the first harvest ($p<0.01$). P levels changed more on Cragieburn structure treatments than Puffers Stream (Fig. 7.8). P concentrations halved between intact and sieved Craigieburn soils compared with only a 0.8 times reduction in Puffers stream soils. The net difference between structure treatments was highly significant ($p<0.001$).

A similar pattern occurred at the second cut with significantly higher P levels on intact soils ($p<0.03$), though overall P concentrations were lower. As before the interaction was not significant (Fig. 7.8). At the third harvest only the difference between soils was significant ($p<0.01$) There were no significant P concentration differences at the fourth harvest between any treatments.

The percentage applied P recovery in plant uptake was estimated to be 54% on Cragieburn and 75% on Puffers Stream soils (Table 7.5). P uptake in roots was estimated from shoot uptake using a ratio of shoot P / total plant P of 0.48 from a similar pot trial (Haynes & Ludecke 1981b). These estimates are probably conservative as the ratio was 0.44 or 0.40 on another pot trial on a similar soil, although at higher P rates (Davis 1981a).

Table 7.5 Recovery of applied P at the first harvest (% applied P).

Soil	Structure		Mean
	Intact	Sieved	
(a) Shoot			
Craigieburn	23.9	27.9	**25.8**
Puffers Stream	35.4	37.0	**36.2**
Mean	**29.7**	**32.5**	
(b) Total Plant			
Craigieburn	49.5	58.7	**54.1**
Puffers Stream	73.3	76.6	75.0
Mean	**61.4**	**67.7**	

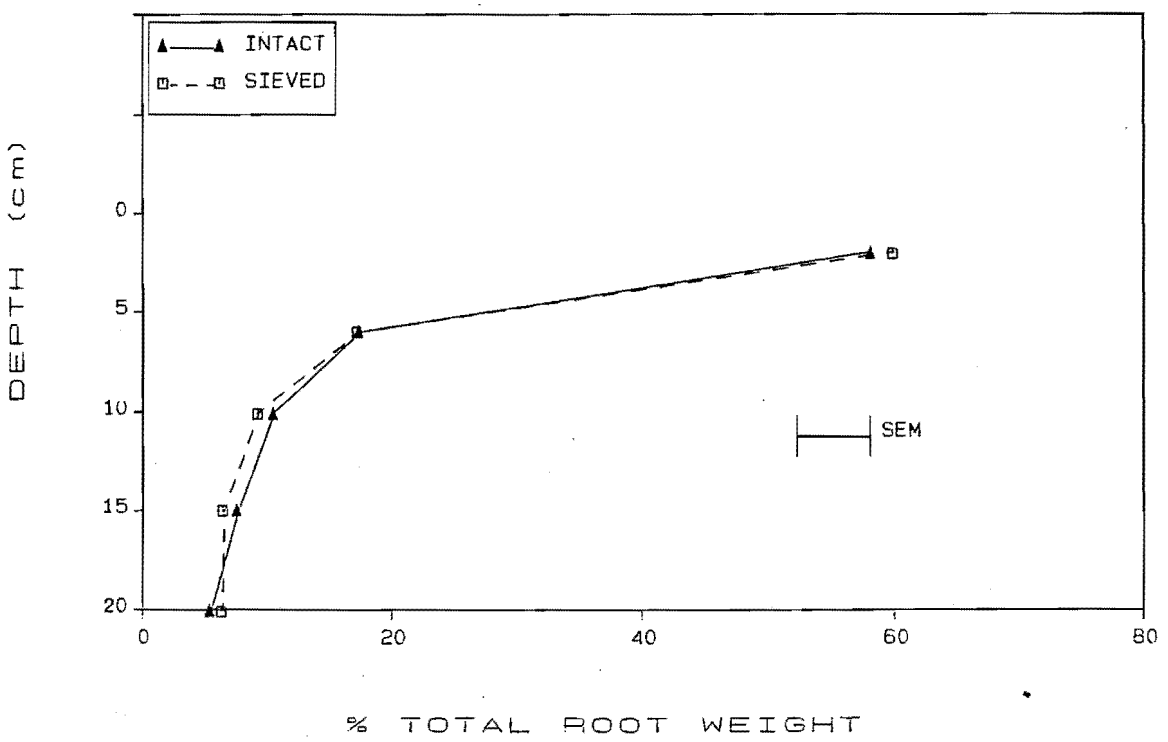


Figure 7.7 : Percentage of total root DM occurring at varying depth in intact and sieved soil cores, cut4.

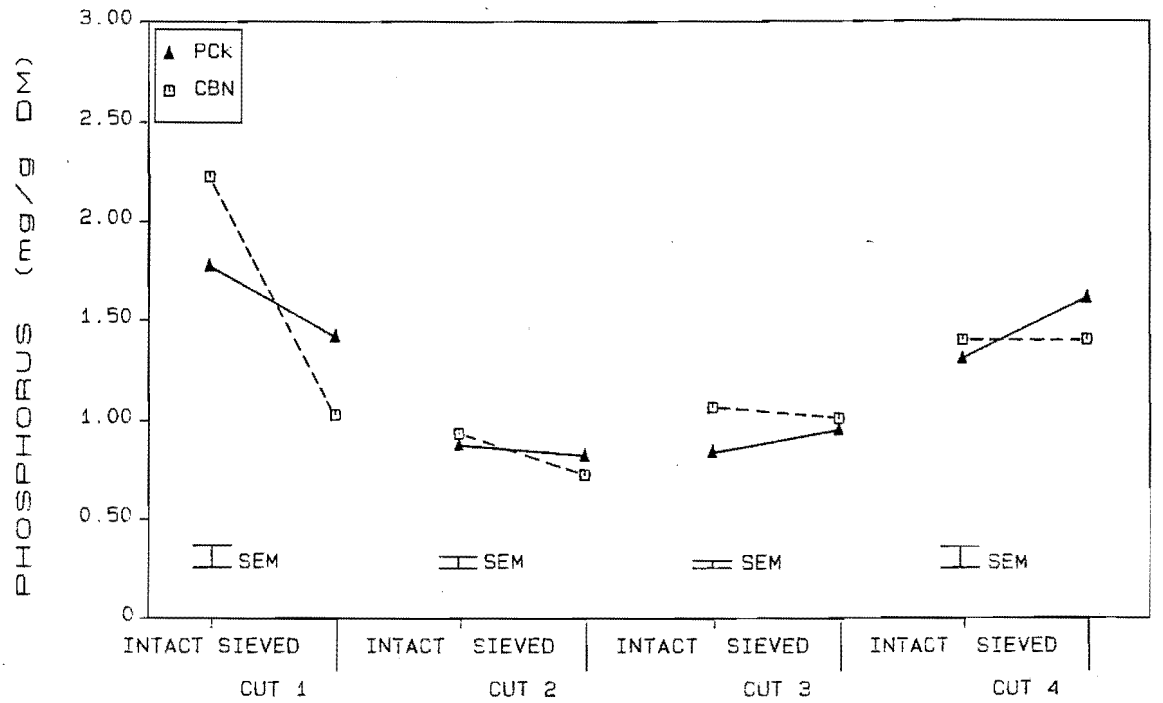


Figure 7.8 : Lotus shoot P concentrations on sieved and intact Puffers Stream and Craigieburn, cut1-cut4.

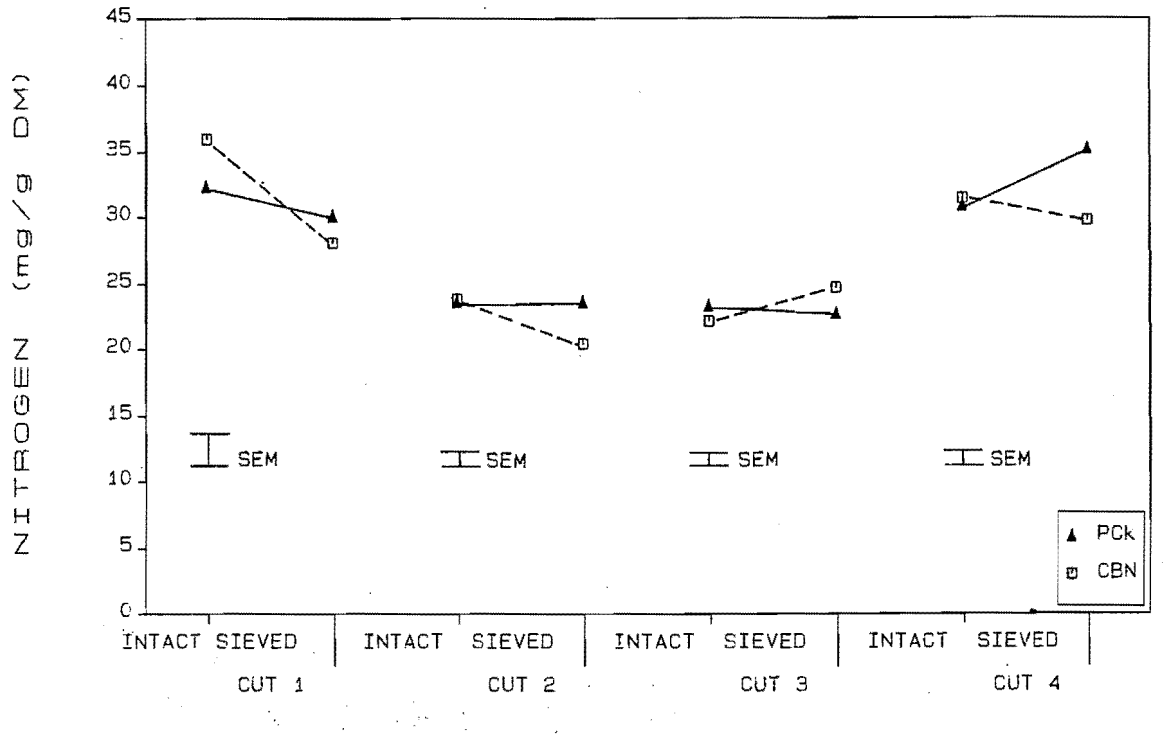


Figure 7.9 : Lotus shoot N concentrations on sieved and intact Puffers Stream and Craigieburn, cut1-cut4.

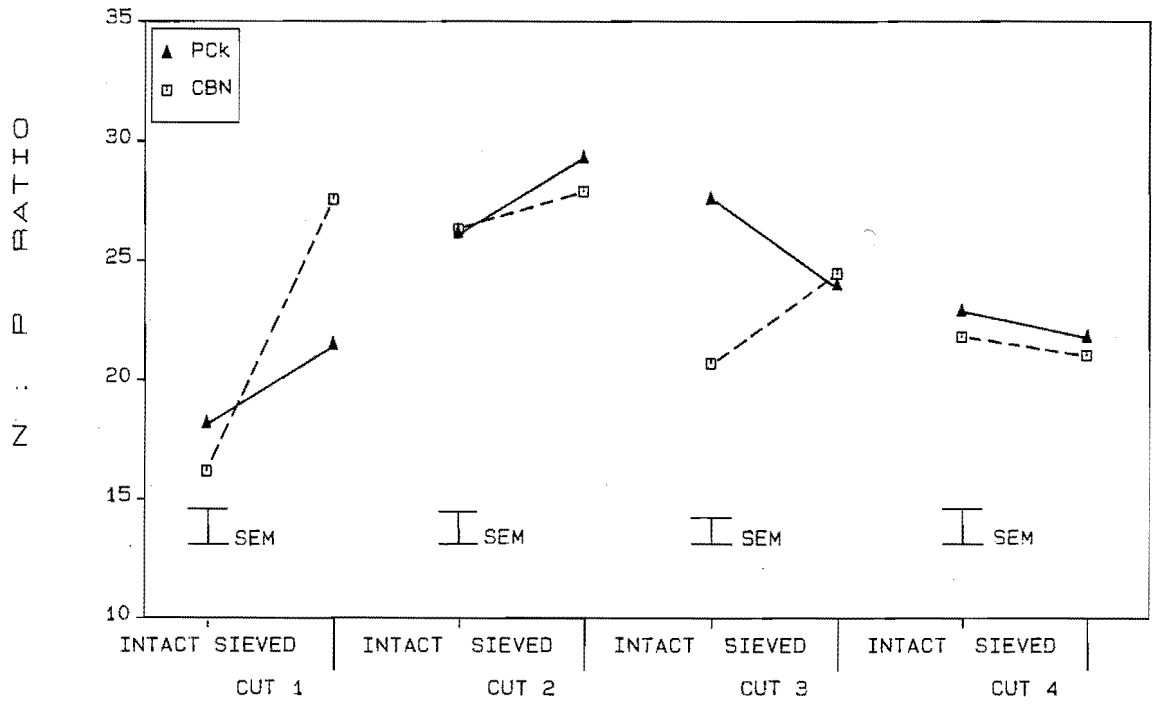


Figure 7.10 : Lotus shoot N : P ratios on sieved and intact Puffers Stream and Craigieburn, cut1-cut4.

Herbage nitrogen concentration patterns were remarkably similar to phosphorus (Fig. 7.9). The decline in N concentration between intact and sieved Craigieburn soils at cut 1 was proportionally greater than in Puffers Stream soils, giving a significant interaction ($p<0.04$). The difference between structure treatments was highly significant ($p<0.001$). As expected, there were no significant differences in N concentrations at the second harvest, following urea application, nor at the third (Fig. 7.9). By the fourth cut however, N levels increased between intact and sieved Puffers Stream soils, while they decreased between corresponding Craigieburn soils ($p<0.02$). The difference between soils was not significant.

Herbage N:P ratios were higher on sieved cores at the first cut ($p< 0.001$; Fig. 7.10). The increase from intact to sieved Cragieburn cores was 1.4 times greater than for the corresponding Puffers Stream cores giving a significant soil by structure interaction ($p< 0.015$). Following N application there were no significant differences between treatments. By cut 3 N:P ratios were significantly higher on Puffers Stream soils ($p< 0.01$). The contrasting response to structure, Puffers Stream ratios decreasing from intact to sieved soils whereas they increased on Cragieburn soils was highly significant ($p< 0.001$). There were no significant differences at the fourth cut.

Total P uptake at the first cut was 1.4 times greater on Puffers Stream soils ($p<0.01$). Differences between structure treatments were not significant nor was the interaction (Fig. 7.11). P recovery dropped at the second cut, intact soils producing 1.2 times the P as sieved soils ($p<0.03$). Uptake at cut 3 increased 1.2 times between intact and sieved Puffers Stream soils in comparison with a slight decrease in Craigieburn soils ($p<0.03$). P uptake was also 1.2 times higher on the Puffers Stream soil ($p<0.001$) The final harvest showed an identical response pattern between soils, no significant difference between them, but a highly significant structure effect ($p<0.001$, Fig. 7.11).

Total Nitrogen uptake was 1.2 times greater on Puffers Stream soils ($p<0.005$) and on sieved soils ($p<0.001$). Nitrogen recovery dropped at the second harvest with no significant differences between treatments or their interaction (Fig. 7.12). Uptake at the third cut was 1.4 times greater on Puffers Stream soils ($p<0.001$) with no significant differences between structure or interaction. At the final harvest sieved cores produced 1.6 times as much N as intact ($p<0.001$) and Puffers Stream 1.2 times that on Craigieburn soils ($p<0.04$). There was no interaction (Fig. 7.12).

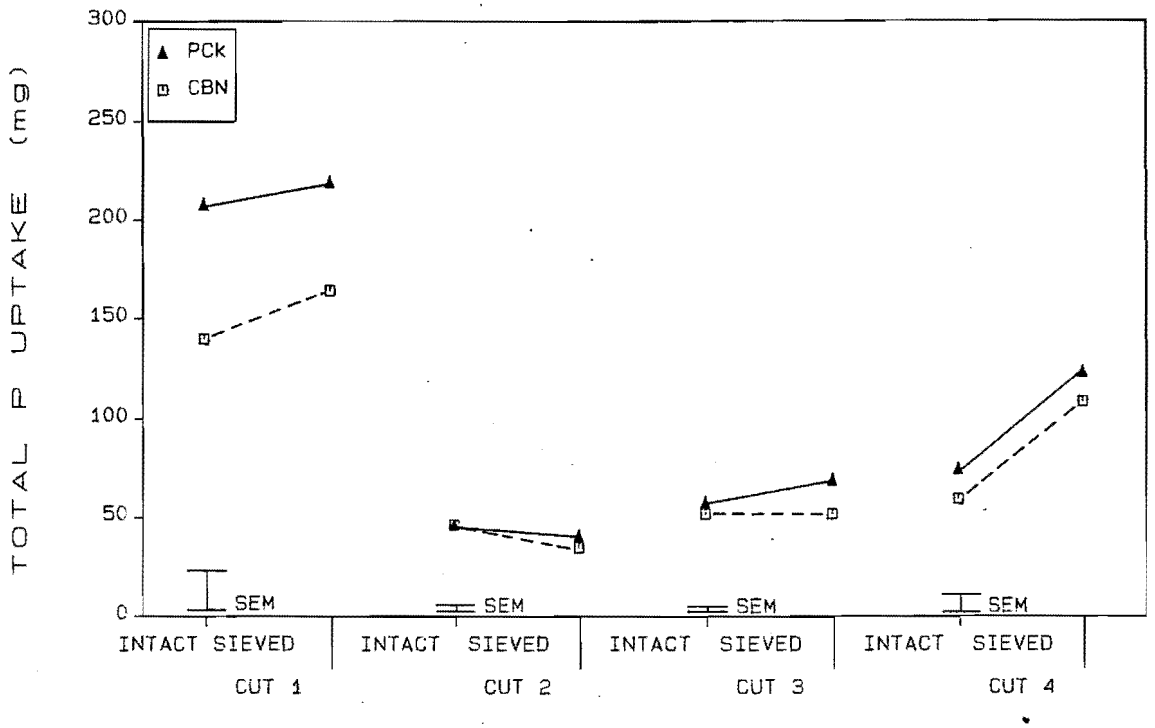


Figure 7.11 : Lotus shoot total P uptake on sieved and intact Puffers Stream and Craigieburn, cut1-cut4.

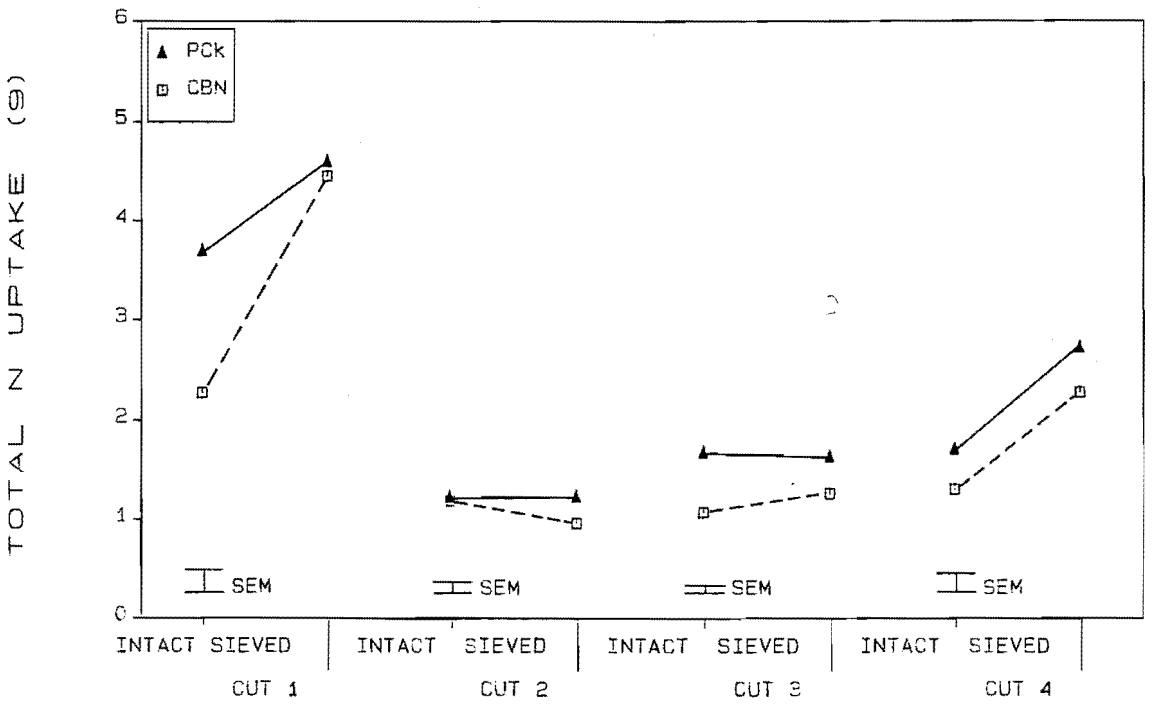


Figure 7.12 : Lotus shoot total P uptake on sieved and intact Puffers Stream and Craigieburn, cut1-cut4.

7.4 DISCUSSION

7.4.1 Resident Vegetation

Resident inter tussock vegetation differed between sites both in species composition and cover (Table 7.1). At Cragieburn cutting four species, sweet vernal, brown top, blue tussock and moss (*Hypnum cupressiforme*) contributed 85% of the ground cover compared with only 25% at Puffers Stream. In contrast, *Raoulia subsericea* and *Coprosma petrei* comprised 70% of the cover at Puffers Stream compared with 2% at Cragieburn. The changes in species composition are similar to those between Puffers stream and Cass (Chapter 1.5.2). Increased precipitation, as shown by the increase in moss, is the primary factor responsible, though edaphic factors, grazing and fire history may also be important.

7.4.2 Stone Content and Bulk Density

The higher stone and gravel content in the Puffers Stream soils (Fig. 7.1) and difference in bulk densities Fig. 7.2) suggests a greater loessial mantle at Cragieburn Cutting and local variation in loess deposition. The accumulation on the surface and in the upper topsoil is evidence for profile truncation by wind erosion. Truncation at Cragieburn is also evidenced by a 60 cm loess column in a buried paleosol compared with 40 cm at the current surface (Tonkin 1981). The deposition history and dynamics of loess within the Waimakariri basin have not been studied and any correlation between the two sites is speculative.

The low regression coefficients and coefficients of determination between stone content and herbage yield (Section 7.3.3) show that reduction in mineral soil volume generally did not significantly affect yield. The only exception, the first harvest on intact Puffers Stream soils, is readily comprehensible considering that the period of initial root development is precisely when effects of reduced topsoil volume would be most pronounced.

7.4.3 Herbage Yield and Mineral Content

The higher dry matter (DM) production on Puffers Stream soils, irrespective of structure treatment, at every cut validates field trial results (Chapter 7.3.3). It clearly demonstrates edaphic factors are responsible for the difference in production. The actual ratio, 1.2 times greater yield on Puffers Stream at the first cut, is similar to the 1.12 fold difference recorded in the field during the first full growing season after establishment, even though duration from planting was not exactly comparable between trials.

The higher Puffers Stream yields in cuts 3 and 4 are probably primarily due to greater availability of P, as shown by the consistently greater total P uptakes (Fig. 7.11). This is consistent with the lower topsoil P retention at Puffers Stream (25% vs 64-73%). The consistently higher N uptakes may also be a direct result of P stimulation of N fixation or N uptake due to the greater growth resulting from the higher availability of P.

The strikingly greater yield of sieved cores compared with intact at the first cut was due to factors associated with nitrogen availability. This was demonstrated by the addition

of urea removing differences between structure treatments at the second and third cuts. Increased N mineralization was probably the single most important causal factor.

Increased N mineralization as a result of air drying was first demonstrated by Birch (1958) and is well supported (Birch 1964, Storrier 1966, Nelson & Bremner, 1972). In New Zealand the phenomenon has been demonstrated in tussock grassland soils in Otago (Tan, 1967, Ross & McNeilly, 1975). In a pot trial with ryegrass (Lolium perenne) herbage yields ranged from 4.3 to 9.5 times greater on sieved air dryed soils compared with seived field moist soils (Ross *et al.* 1978). The soils used were Cluden and Tima southern yellow grey earths (YGE), (Molloy & Blakemore, 1974). The same effect occurred with a Carrick high country yellow brown earth (YBE) though the difference was smaller (2.8 times). On all soils these ratios gradually declined with subsequent harvests.

Addition of fertilizer N reduced the difference between air dryed and moist soils to between 1.6 - 2.8 times on the Tima & Cluden soils and 1.5 on the Carrick. Interestingly the difference between treatments was less when the soils were sampled under ryegrass-white clover pasture or fescue tussock grassland only 100 m apart. Under tussock the mean difference was 9.1 fold compared with 4.1 fold under pasture, averaged across the two yellow grey earths. These ratios dropped to 2.0 and 1.6 times respectively when fertilizer N was added.

A concurrent incubation experiment showed N mineralization appreciably increased with air drying and also by addition of P,K and S fertilizers (Ross & Bridger, 1978b). However the addition of P,K and S did not increase subsequent N mineralization on the pasture samples. There were highly significant correlations between the amount of mineral N produced in incubated soils and ryegrass yield and N content in the pot trial. Surprisingly the N mineralization rates of these soils could not be directly related to counts of ammonifiers (Ross & Bridger 1978b).

A further experiment, using the same soils, confirmed these results (Ross *et al.*, 1979).

Sieving itself can slightly increase mineral N content though the effect is small compared with air drying (Ross & Bridger 1977). The effect was demonstrated in a Taita central YBE under pasture and in a sequence of nine tussock grassland soils (Ross *et al.* 1979a).

The physical properties of sieved soils were also superior to those in the intact cores. The lower surface compaction (Table 7.4), horizon bulk densities (Fig. 7.2) and greater aggregate disruption would allow easier root penetration and ramification (Hillel, 1983). The greater air filled porosity in sieved soils would give better aeration and gas exchange plus a greater availability of soil water at lower suctions (Bunt 1961, Handreck 1983). The rate of water flux through the soil would also have been faster. These conditions would be more favourable for nodulation, N fixation and root nutrient uptake (Marschner 1983).

Differences in soil C:N ratio also probably contributed to the differences between intact and sieved soil. All coarse, medium and as many fine roots as possible were removed from the sieved soils but left undisturbed in the intact cores. Root C:N ratios are only

available for fescue and blue tussocks: ratios were very high, 67 and 71 respectively (Ross & Cairns 1980). When standing dead or root material was directly added to soil from these tussocks (and also three species of *Chionochloa*) they inhibited N mineralization but had little effect on net nitrification (Ross & Cairns, 1980). There was no evidence that litter or roots of any tussock was markedly inhibitory; the effect was attributed to immobilization resulting from the wide C:N ratios. Ross (1958, 1960a) earlier reported fescue tussock roots from Cragieburn to have no deleterious effect on N mineralization.

Scott (1975) investigating allelopathic influences of tussock grassland species, found green shoot or root material of fescue and blue tussocks generally had little effect on legume or grass germination but sweet vernal, and to a lesser extent browntop, depressed germination of grasses.

It is likely therefore, though this has not been demonstrated, that the main effect of residual root material in the intact cases was not allopathic. It is far more likely it depressed or inhibited nitrification by virtue of high C:N ratios (Harmsen & Van Schreren, 1955) in a similar way as demonstrated with tussock species (Ross & Cairns 1980).

If this is the case it might further be conjectured that the greater ramification of the finer grass roots in the Cragieburn cores compared with the lower density of coarser roots in the forb-dominated Puffers Stream cores would have resulted in more extensive N immobilisation in the Cragieburn cores. This explanation is consistent with the markedly lower yields of the Cragieburn intact cores relative to Puffers Stream at the first cut and then their close similarity after addition of N at the second cut (Fig. 7.3).

Another possible explanation for the soil by structure interaction is higher levels of mineralisable substrate were present at Puffers Stream, analagous to the differences between pasture and tussock demonstrated by Ross *et al.* (1978a,b). Differences in total soil nitrogen between Cragieburn and Puffers Stream are small (0.32 vs 0.34%).The slightly higher Puffers Stream N level is probably of little consequence as higher total N levels were present in tussock (0.26%) than pasture (0.21%) in a Tima soil yet pasture gave greater ryegrass herbage and N yields (Ross *et al.* 1978a). Robinson (1962, 1963) and McSweeny (1983) both found very low mineralization occurring in Waimakariri Cragieburn soils near the Cave Stream site, consistent with the small populations of nitrifiers and very low rates of nitrification observed in strongly to moderately acid tussock grassland soils (Ross 1958, White 1959, Tan 1967).

Whatever the precise mechanism, it is clearly evident from the abrupt removal of all treatment affects by N addition after Cut 1 (Fig. 7.3) that factors related to N availability were responsible for the differences between soils and structure treatments in the first harvest. Evidently the increase in $NaHCO_3$-extractable P, attributed to microbial death following air drying demonstrated in a wide range of New Zealand Soils by Sparling (1985) or the increased capacity to sorb P following air drying (Haynes and Swift, 1984) were small compared with the effect of the added fertilizer P. Similarly changes in cation and anion exchange capacity, potassium and magnesium adsorption following air drying are likely to be negligible (Phillips *et al.* 1986). If present, they would also be marked by basal fertilizer levels.

The surprising reduction in herbage yields after the first harvest (fig. 7.3) is partially due to the shorter period between harvests, slower growth following depletion (Sheath 1960b) and also a probable decrease in nutrient availability.

The mean daily growth rate, averaged over all treatments, was 1.05 g DM day^{-1} to the first cut, 1.17 g DM day^{-1} to the second and third cuts and 0.33 g DM day^{-1} for the forth. As the first cut growth rate was averaged from germination to the onset of flowering it appears lower than subsequent rates. Nevertheless the actual growth rates immediately prior to harvesting must have been high to give an average rate for the whole period not much lower than subsequent rates. The low growth rate at the fourth cut is due to slow growth over winter and harvesting in early spring before the main acceleration in growth occurred.

Nitrogen application in spring stimulated growth of lotus seedlings establised the previous autumn (Charlton & Brock 1980). Applying N within a week of germination in a pot trial increased growth and N fixation (Wedderburn 1983). However N application at sowing in tussock grassland decreased lotus nodulation and yield (Wedderburn 1986). Yield depression was linearly related to increasing N levels. Hall & Scott (1985) unexpectedly found N rates in excess of 40 kg N ha^{-1} did not further increase legume production. Whether the high N rate (120 kg N ha^{-1}) applied to cores had a similar effect is not known.

The evidence for nutrient limitation after the first cut is both direct and inferential. The direct evidence is the lower total nutrient recovery and higher N:P ratios after Cut 1. Over 25% and 35% of applied P was removed in Cragieburn and Puffers Stream shoot herbage at Cut 1, assuming minimal supply from labile P pools in each soil. The total P recovered by lotus is conservatively estimated at 53% and 75% for each soil (Table 7.5). The difference in P recovery rates is inversely related to soil P retention 67% and 24% and directly correlated with intensity of P sorption on soil colloids. Though less applied P was removed in Cragieburn shoots a greater proportion would be sorbed on colloids and thus total P available to plants would probably be low. Furthermore Mitchell (1958) showed the rate of nutrient release from degradation of lotus root systems after defoliation was much slower than that of clover. Thus it is quite possible a large proportion of organic P in root systems was not immediately available following the first cut and only gradually became available as it was mineralized. This explanation is consistent with the gradual increase of total P uptake in the third and fourth cuts.

Further evidence for decreased P availability after the first cut and gradual improvement in P status is seen in N:P ratios. (Fig. 7.10). The ratios peaked at the second cut at levels twice those regarded as indicative of P defficiency by McNaught (1970), before gradually decreasing at the third and fourth cuts. The effect of other nutrient availability, e.g. sulphur and cations, is unknown, but considering the high basal levels, are not likely to be limiting.

Shoot N & P tissue contents follow a remarkably similar pattern (Figs. 7.8 & 7.9). The lower contents in the sieved soils at the first cut is due to growth dilution. The lower P levels in the second cut and the generally similar levels in the third cut suggest limitations in P supply, as discussed.

The absence of increased shoot N levels following urea application is surprising. Reasons for this are unclear: possibly it is due to P limitation affecting uptake or maintenance of internal N homeostasis. The high N and P contents in the fourth harvest are typical of high nutrient contents found in early spring herbage prior to the nutrient demand of spring growth (Metson & Saunders 1978a,b, Hay *et al.* 1985).

7.5 CONCLUSIONS

Standard pot trial soil preperation techniques grossly affected lotus herbage production and nutrient uptake. Air dried sieved soil had lower surface and bulk density, lower stone content, higher seedling establishment and gave consistantly higher herbage, N and P yields compared with intact cores. Proportionatly more roots occured in the topsoil and less in the subsoil of intact cores. Nitrogen addition removed the differences in plant response strongly suggesting increased N mineralization following air drying was largely responsible. Improved physical structure also contributed.

Puffers Stream soils differed from Cragieburn soils. They consistently produced higher legume yields and uptake of N and P. They showed less response to air drying and sieving than Cragieburn soils. These differences are consistant with pedological development. Higher levels of reactive alumimosilicate colloids giving greater P retention and lower P availability is suggested as the primary causitive factor.

These results disprove the working hypothesis and show pot trials with Cragieburn high country yellow brown earths can not be used with confidence to predict field responses.

CHAPTER 8 PHOSPHATE RESPONSE OF *LOTUS PEDUNCULATUS* AND *TRIFOLIUM REPENS* ON FOUR POTTED HIGH COUNTRY YELLOW BROWN EARTH SOILS.

8.1 INTRODUCTION

A major objective of this thesis is to compare the agronomic performance of *Lotus pedunculatus* cv. 'Grasslands Maku' (lotus) and *Trifolium repens* cv. 'Grasslands Huia' (clover) on moderately acidic high country yellow brown earth soils (Chapter 7.1). To do this soils were investigated spanning a wide range of the pedological developement found in montane eastern South Island soils (Chapter 1.4). However comparison of legume P response in field trials at each end of the developement sequence was confounded by climatic differences between sites and possibly by within-site microclimatic variation (Chapter 1.3).

Therefore the working hypothesis investigated in field trials that:

'lotus herbage production will be greater than clover, and that the relative difference in yield will be inversely related to P availability and will increase with soil pedological development'

was also tested under uniform glasshouse conditions to remove climatic effects and allow direct comparison of edaphic factors.

8.2 MATERIALS AND METHODS

8.2.1 Experimental Design

The experimental design was randomised complete block factorial with two legumes, four soils and five phosphate fertilizer levels. Soils, phosphate and legumes were the same as those used in field experiments (Chapter 6). Treatments were replicated in five blocks, giving a total of 200 pots. The specific treatments were:-

(A)	Legume	: *Trifolium repens*	cv. 'Grasslands Huia'.	
		: *Lotus pedunculatus*	cv. 'Grasslands Maku';	
(B)	Soil	: Puffers Creek	T1, T4, T5	
		: Craigieburn	CB4;	
(C)	Phosphate	: 0, 25, 100, 400 kg P ha^{-1}	with	Basal
		: 100 kg P ha^{-1}	without	Basal

8.2.2 Soils

Soils were sampled from the main surfaces at the Craigieburn and Puffers Stream study sites on 29 May and 6 June 1982 (Chapters 1.4, 7.2). Vegetation immediately adjacent to the main soil pit on terrace one (T1) four (T4) five (T5) and Craigieburn Cutting (CBN) was carefully removed and the upper Ah horizon excavated to 10 cm. Soils were air dried for 2 weeks in a Lincoln College glasshouse and prepared as described in Chapter 7.2.

Air dry soil, equivalent to 1.2 kg oven dry soil, was weighed (± 0.2g) into 15 x 15 cm polythene pots with an impervious plastic liner (Table 8.1). The weight of water retained in free draining containers 24 hours after complete submersion ('Field Capacity') was determined in triplicate. The amount of water required to bring soils to 80% of this value was determined (Table 8.1). All pots were watered to weight (± 0.1 g) with deionized water on the 24 June prior to fertilizer application.

Table 8.1: Pot preparation parameters

Soil	% H_2O held at 'Field Capacity'	Pot Weight at 80%'Field Capacity'
T1	31.4	1784
T4	40.7	1931
T5	37.1	1819
CB4	46.5	2226

Four phosphorus treatments, designated P_0 to P_{400}, were applied on 25 June at rates of 0.0, 25.0, 100.0 and 400.0 by P ha^{-1}. Potassium dihydrogen orthophosphate (Analar grade) was the P source, with 0.0, 0.033, 0.133 and 0.513 g orthophosphate per pot applied in solution by pipette (10.0 ± 0.1 ml). Basal fertilizers were applied to all pots on 26 June, except the fifth treatment of P_{100} minus basal, as follows:

Fertilizer (Analar Grade)	Form	Rate (kg ha^{-1})	Elemental Rate (kg ha^{-1})			
Gypsum	$CaSO_4.2H_2O$	20	Ca	5.89	S	4.71
Potassium Sulphate	K_2SO_4	50	K	22.44	S	9.20
Magnesium Sulphate	$MgSO_4.7H_2O$	100	Mg	20.19	S	26.64
Sodium Molybdate	Na_2MoO_4	0.4				
					S	40.55

Fertilizers were applied in solution by pippette (10 ± 0.1 mm) except for gypsum which was mixed with sand and spread by hand.

Lotus pedunculatus cv 'Grasslands Maku' and *Trifolium repens* cv 'Grasslands Huia' were inoculated with 'Nodulaid' and 'Rhizocote' rhizobid respectively at recommended commercial rates immediately prior to sowing on 1 July. Twenty seeds were sown per pot and lightly watered. Seedlings were thinned to 10 plants per pot one month later (5 August) when the first trifoliate leaves appeared.

Pots were watered to weight weekly during July with an electronic balance (± 0.2g) and at 5 day intervals during August. Watering rates were increased on 2 September to compensate for plant growth and frequency increased from watering every three days at the beginning of the month to daily at the end. Plants were watered daily in October though weighing was impracticable and set volumes of water were substituted. Low P treatments initially received 25-50 mm per watering and high P, 200 mm, rising by the end of the experiment to 100 mm for low P and to 250 mm between 7-12 Oct and 300 mm between 13-20 Oct for high P treatments.

Harvesting (19 - 21 October) commenced with the first flowering, 15 weeks after sowing. Aerial herbage, hereafter termed shoot (lamina + petiole + stem), was cut off at ground level by scalpel and immediately dried in a forced draught oven for 48 hours at 68-79 °C. Samples were weighed (± 0.1 g) and chemically analysed as specified in Chapter 6.2.

Roots were gently hosed free of bulk soil then washed for 30 minutes in a 0.25 mm rotary sieve pressure spray system. Cleaned samples were refrigerated at 3 °C while unseparated fine roots and detached nodules were stored in 1% formalin solution. These samples were individually hand separated in the laboratory from fine sand and added to the original sample. Roots were oven dried and treated similarly to shoots.

8.3 RESULTS

8.3.1 Dry Matter Production

(a) Shoot and Root Production

Phosphorus had the greatest effect of all treatment factors on dry matter (DM) production (Table 8.2; Plate 8.1).

Table 8.2: Effect of treatment on DM production (ANOVA % Sum of Squares and significance)

Factor	Shoot		Root		Total		R:S Ratio	
Phosphate	95.0	***	52.8	***	91.9	***	17.9	***
Legume	1.2	***	0.8	*	1.2	***	1.0	NS
Soil	1.9	***	9.5	***	2.0	***	8.5	***
Phos. x Leg.	0.3	**	1.1	NS	0.5	***	2.9	*
Phos. x Soil	1.5	***	2.2	NS	1.5	***	22.3	***
Leg. x Soil	0.1	NS	0.1	NS	0.1	NS	1.4	NS
P x L x S	0.3	NS	0.6	NS	0.3	NS	4.3	NS

significance: $p < 0.05$ * ; $p < 0.01$ ** ; $p < 0.001$ ***

Shoot DM is used in the following discussion in preference to total DM as it was not confounded with extraneous root material, mainly residual browntop roots, which could not be completely seperated. Shoot DM was the principal component of total DM and identical in response to treatment factors (Table 8.2).

The shoot DM interaction between P and soil, averaged for both legumes since the legume by soil interaction was not significant, is shown in Figure 8.1. The interaction is due to the different change in DM production per incremental change in applied P, i.e. the change in slope of the soil P response. To assist interpretation of Figure 8.1 these changes are also tabulated in Table 8.3.

Table 8.3: Incremental change in shoot DM production per unit applied P (g DM / kg P ha $^{-1}$).

SOIL	APPLIED P 0-25	25-100	100-400
T 1	0.46	0.12	0.009
T 4	0.32	0.14	0.016
T 5	0.26	0.11	0.019
CB4	0.43	0.15	0.016

The interaction can be explained as follows : between P_0 and P_{25}, P response was greater on T1 and CB4 than on T4 and T5. Between P_{25} and P_{100}, T1 and T5 responded less than CB4 and T4, but between P_{100} and P_{400}, T4, T5 and CB4 all continued to respond more strongly than T1.

The legume by P interaction (Table 8.2) is due to the greater lotus P response between P_0 and P_{25} while clover P response between P_{25} and P_{100} exceeded that of lotus (Fig. 8.2).

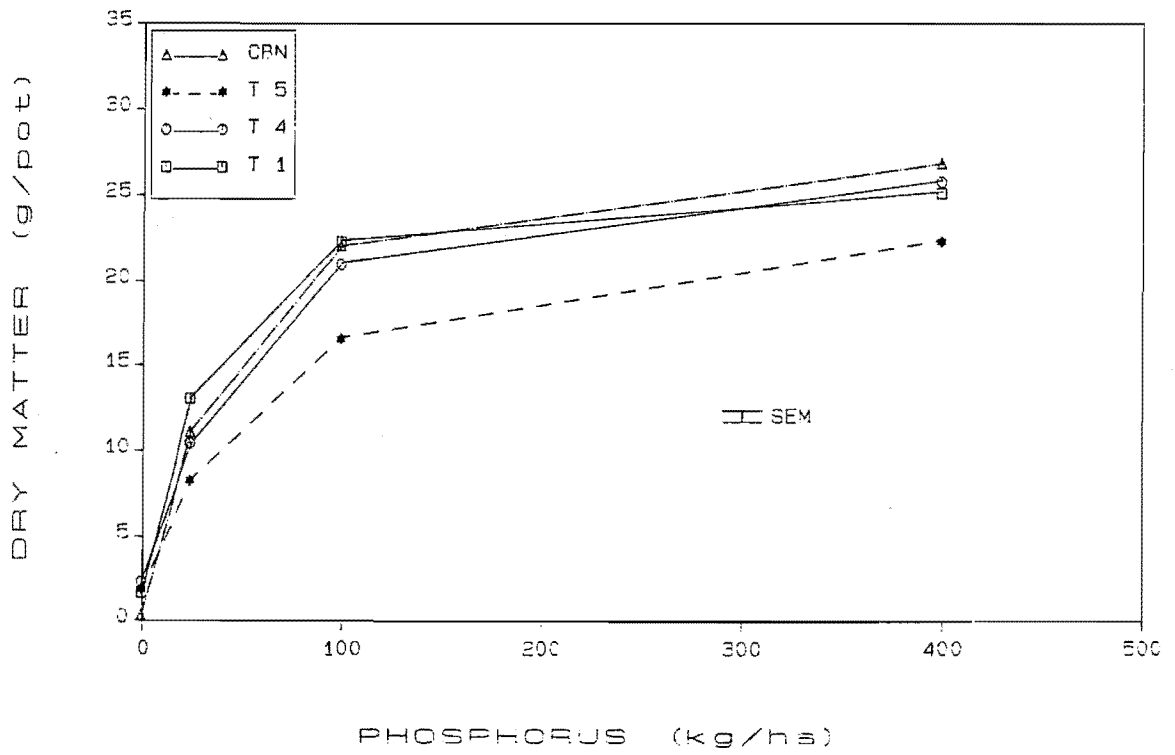


Figure 8.1 : Legume shoot DM response to 0-400 kg applied P ha^{-1} in soils T1-CB4

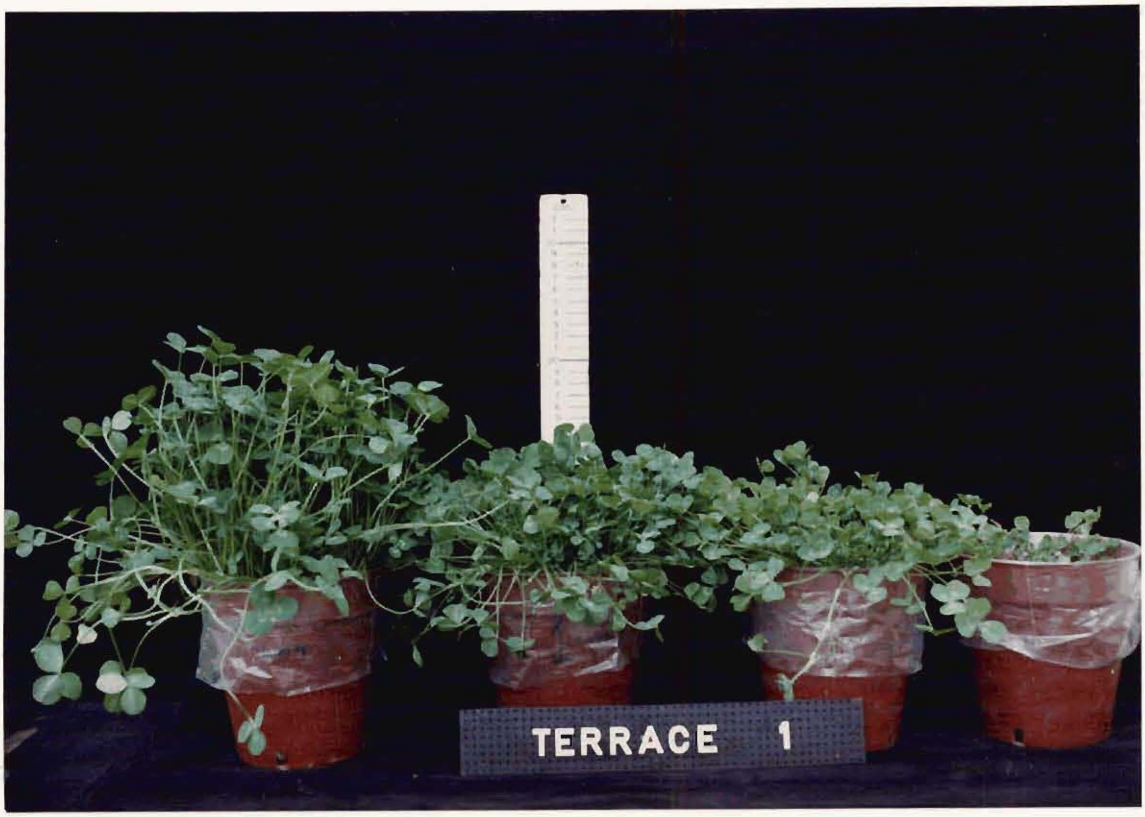


Plate 8.1 : The effect of 0 - 400 kg applied P ha^{-1} on clover shoot DM production on T1

Figures 8.1 and 8.2 illustrate the main treatment effects: the highly significant P response by both legumes, lotus outyielding clover at all P rates and the difference in production on different soils, T5 yielding markedly lower than the other soils.

Root DM increased with P application with the greatest response occuring before P_{100} ($p < .001$; Fig. 8.3). Lotus root yield was greater than clover except for P_0 ($p < .001$) though this difference did not cause a significant legume by P interaction ($p > .08$).

Root production was greater on Craigieburn soils with little difference between Puffers Stream soils ($p < .001$; Fig. 8.4). The legume by soil interaction was not significant ($p > .840$).

Root: shoot ratios were higher at low P rates ($p < .001$) with significant differences between soils ($p < .001$; Fig. 8.5). Greater root production relative to shoots occurred at P_0 in all soils excepting T1. The extremely high ratio of 7.7 at P_0 in Craigieburn soils, is an artifact due to incomplete separation of resident roots. Craigieburn soils have much higher quantities of fine grass roots (Chapter 8.3) relative to Puffers Stream, and this, coupled with the extremely low shoot production (Fig. 8.1) produced the inflated ratio. Nevertheless, the trend in root:shoot ratio is undoubtedly correct. The true Craigieburn ratio is likely to be greater than, or similar to, T5.

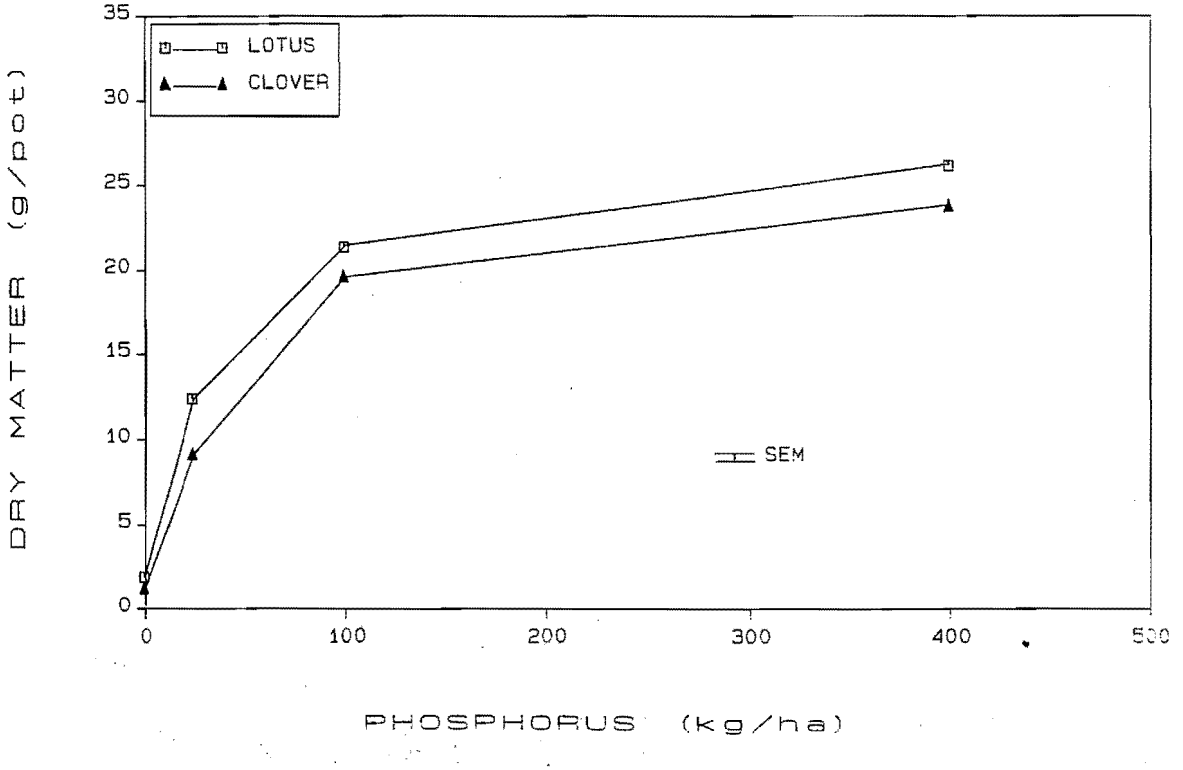


Figure 8.2 : Lotus and clover shoot DM response to 0-400 kg applied P ha^{-1}

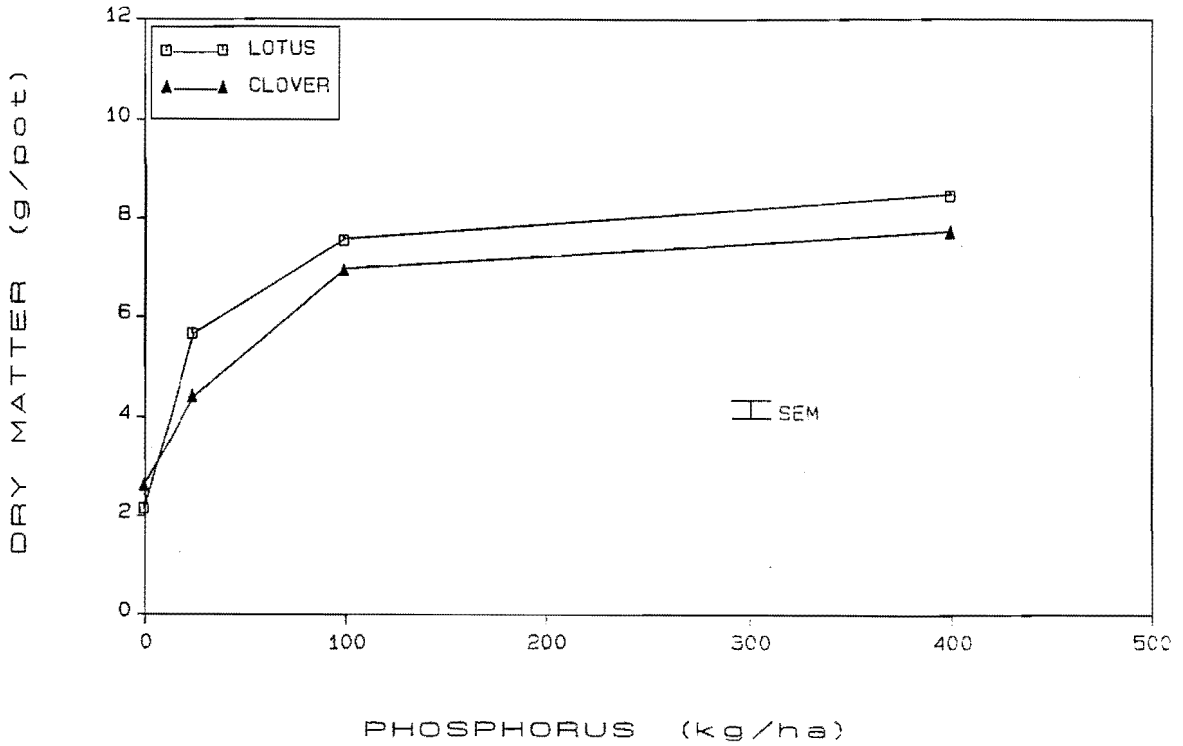


Figure 8.3 : Lotus and clover root DM response to 0-400 kg applied P ha^{-1}

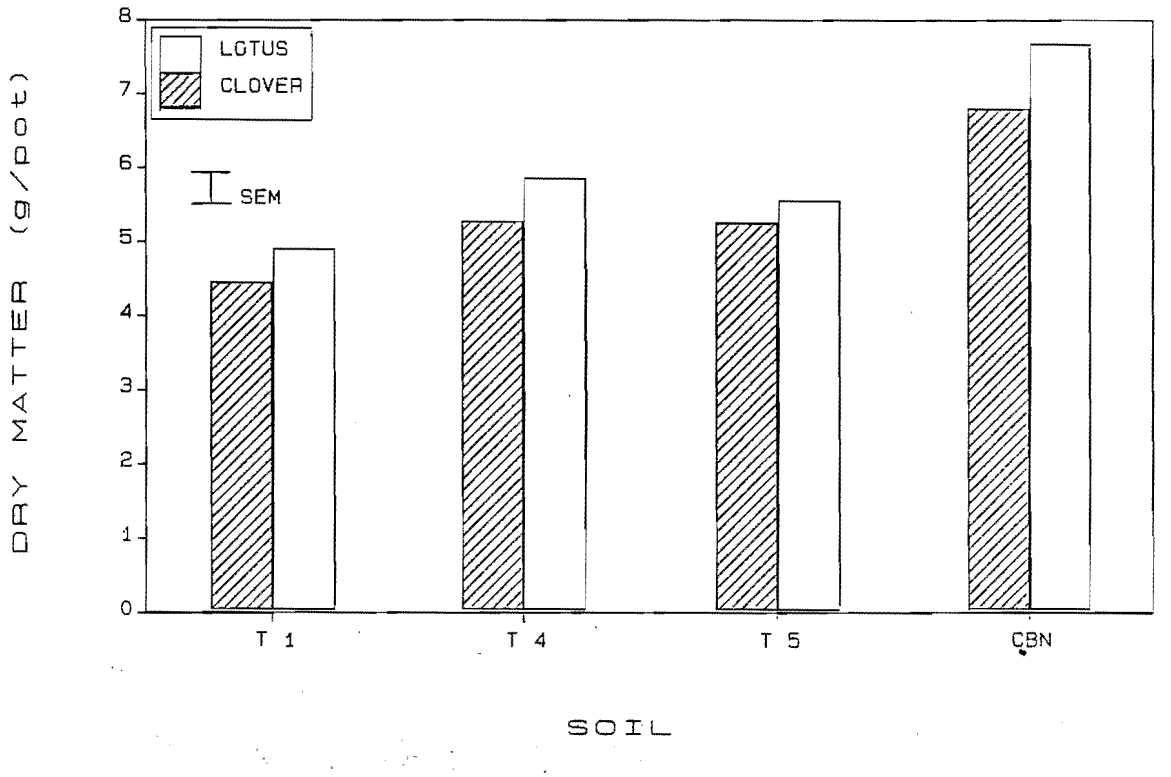


Figure 8.4 : Lotus and clover root DM production on soils T1 - CB4

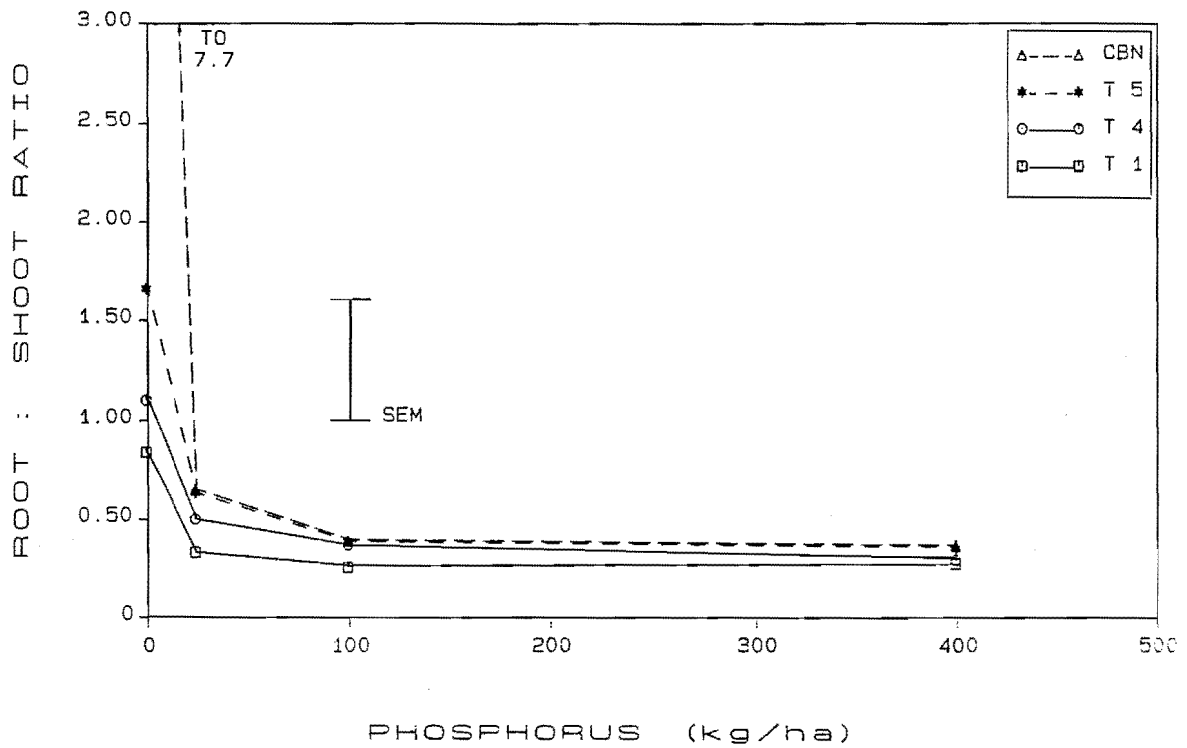


Figure 8.5 : The effect of 0-400 kg applied P ha^{-1} on root: shoot ratio on soils T1-CB4

(b) Production and Soil Chemistry

Soil chemical properties (Ah horizon: 0-10 cm) are summarised in Table 8.4. Correlation between soil chemical variables shoot and root DM, as determined for fescue tussock (Chapter 4.3), are listed in Table 8.5.

Table 8.4: Topsoil (0 - 10 cm) chemical variables in Craigieburn and Puffers Stream soils.

Variable #	Soil			
	T1	T4	T5	CB4
pH	5.9	5.5	5.5	5.9
pHCl	5.0	4.8	4.7	4.4
Si_o	0.04	0.03	0.03	0.10
Fe_o	0.34	0.53	0.28	0.82
Al_o	0.38	0.70	0.46	0.76
Al_p	0.20	0.38	0.18	0.51
Fe_p	0.14	0.36	0.28	0.35
Al_e	0.032	0.066	0.04	-
Fe_e	0.012	0.017	0.016	-
NaF	9.2	9.2	8.8	9.7
Pret	27	44	30	72
Pxrf	92.9	110.67	62.3	-
Ptot	77	113	59	89
Pap	21	39	19	28
Porg	53	72	37	59
LOI	11.7	14.4	9.26	-
C	3.5	6.6	3.3	5.9
N	0.25	0.32	0.19	0.38
S ##	4	4	3	5
CEC	15.0	22.7	16.0	20.0
ECEC	8.7	9.5	8.0	75
BS_C	56	38	38	33
BS_E	97	91	75	85
Ca	6.7	5.8	4.6	4.6
Mg	0.9	1.4	0.7	0.6
K	0.68	1.33	0.55	1.10
Na	0.08	0.07	0.10	0.05
Al	0.2	0.6	1.7	1.0
H	0.1	0.3	0.3	0.1

Variable codes are defined in Appendix 2.2
MAF quick test index only: not used in correlation analyses.
(source: Harrison and Swift 1984)

Table 8.5: Correlation of soil chemical parameters and legume DM (Pearson Correlation Coefficient r & significance probability, SAS 1986).

(a) **Shoot DM**

Clover	Al	BS_E	TEB	Pxrf	Ca
	-.98	.97	.875	.79	.78
	(.02)	(.02)	(.12)	(.42)	(.22)
Lotus	Pxrf	Na	Al	N	NaF
	.90	-.84	-.82	.83	.83
	(.29)	(.16)	(.17)	(.17)	(.17)

(b) **Root DM**

Clover	pHCl	Fe_e	Pret	Fe_O	Si_O
	-.98	.98	.95	.88	.85
	(.092)	(.12)	(.05)	(.12)	(.14)
Lotus	Fe_e	Pret	pHCl	Fe_O	Al_p
	.99	.98	-.95	.93	.90
	(.07)	(.02)	(.05)	(.07)	(.09)

(c)Comparison of Field and Glasshouse Results

In order to compare results from the field and glasshouse experiments (Chapters 6 & 7) with this experiment, shoot DM yields were all scaled relative to yield on T4 (Table 8.6). The comparison is only approximate as duration and physiological development at harvest differed between experiments. The Puffers stream field trial was harvested in early autumn, after flowering ceased, 16.5 months after seedling transplantation. The Craigieburn field data were harvested in early summer 12 months after transplanting. There were also some slight differences in P levels (Chapters 6.3 and 7.3). The soil structure experiment (Chapter 7) and this pot trial were in the same glasshouse synchronously, and were both harvested at the onset of flowing. These results are thus directly comparable.

Table 8.6: Comparative shoot DM production in field and glasshouse experiments (DM relative to T4 DM; CB4 Field Data, Kee (1981)..

Experiment	Soil			
	T1	T4	T5	CB4
(a) Lotus				
Field Trial	0.1	1.0	0.6	0.8
Structure Expt - Sieved	-	1.0	-	1.03
Structure Expt - Intact	-	1.0	-	0.5
Pot Trial	1.0	1.0	0.8	1.03
(b) Clover				
Field Trial	0.1	1.0	0.6	0.6
Pot Trial	1.1	1.0	0.8	1.0

(d) Basal Fertiliser Effect

Basal fertilizers had a significant effect on DM yield (Table 8.7).

Table 8.7: Effect of Basal Fertilizer on DM production (ANOVA % Sum of Squares and significance probability).

Factor	Shoot		Root		Total		R:S Ratio	
Basal	89.8	***	60.8	***	85.6	***	47.3	***
Legume	2.4	***	4.2	**	2.3	***	0.1	NS
Soil	7.7	***	7.4	**	8.1	**	10.7	*
Basal x Legume	0.0	NS	0.0	NS	0.0	NS	0.3	NS
Basal x Soil	3.8	***	15.5	*	3.7	***	16.9	**
Legume x Soil	1.1	NS	3.7	NS	0.9	NS	7.3	NS
Basal x L x S	0.3	NS	0.8	NS	0.5	NS	3.8	NS

The interaction between basal and soil with shoot DM production is due to the greater decrease in yield on Craigieburn and T1 soils when basal fertilizers were not supplied ($p < .001$, Fig. 8.6). Lotus shoot yield was greater than clover both with (21.5 vs 19.7 g pot^{-1}) and without basal (9.8 vs 7.7 g pot^{-1}; $p < .001$) (Plates 8.2, 8.3). Lotus also outyielded clover on all soils. The soil by legume interaction was not significant ($p < .065$) though species performance differed on Craigieburn soil (Fig. 8.7).

The root DM basal by soil interaction was very similar to the shoot interaction. The cause was again the greater decrease of Craigieburn yields, without basal, relative to other soils ($p < .05$; Fig. 8.8). Comparing root to shoot ratio (R:S) the highly significant ($p < .007$)

Plate 8.2 : The effect of basal fertiliser on lotus shoot DM production on CB4

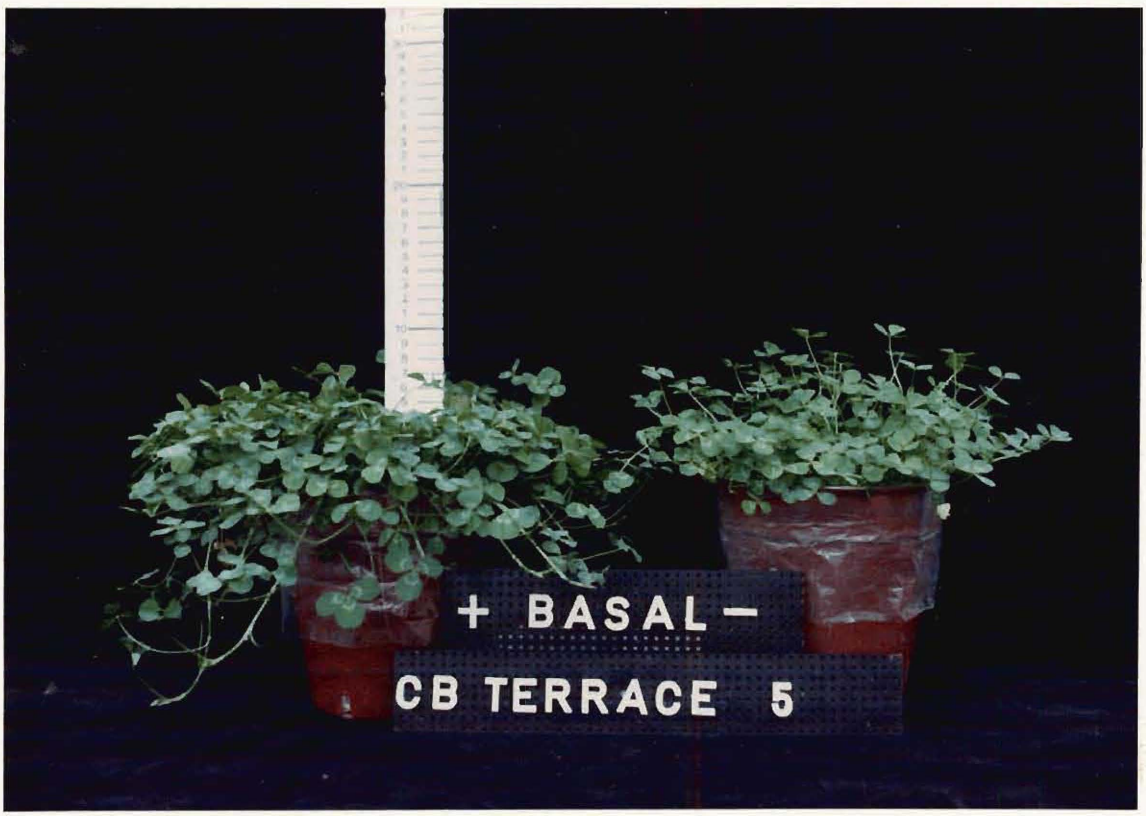


Plate 8.3 : The effect of basal fertiliser on clover shoot DM production on CB4

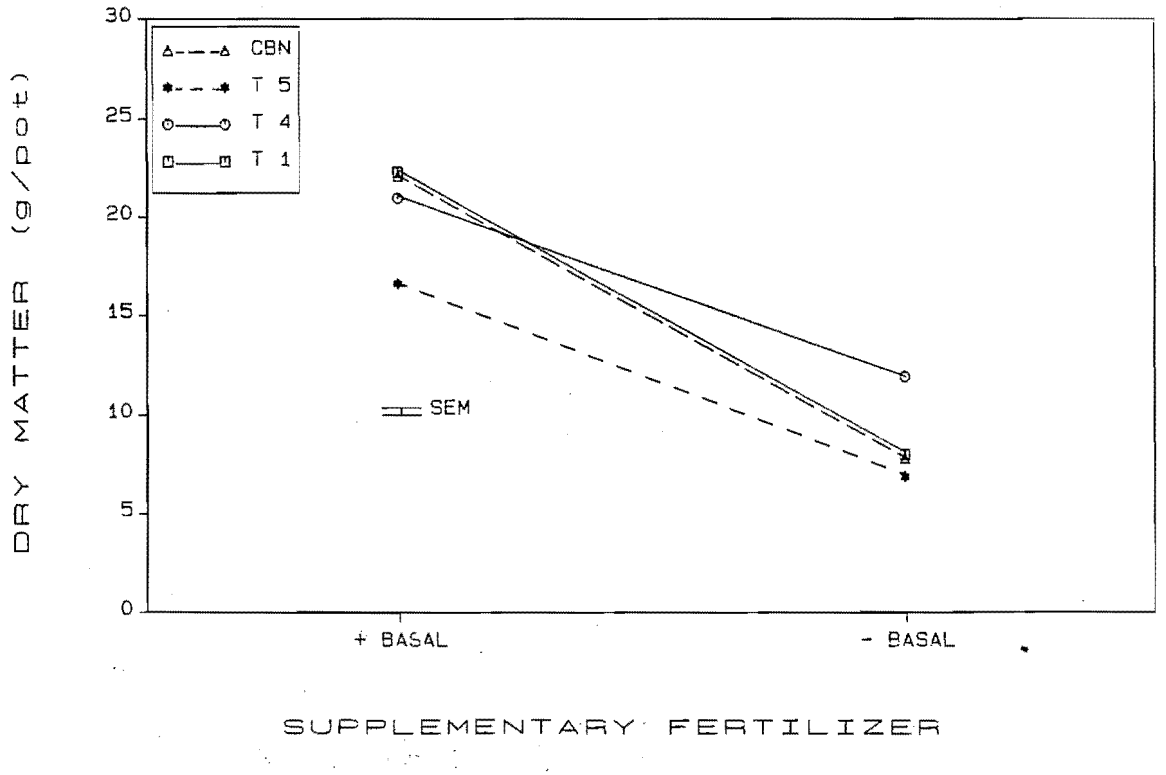


Figure 8.6 : The interaction between basal fertilisers and soil with Shoot DM (g)

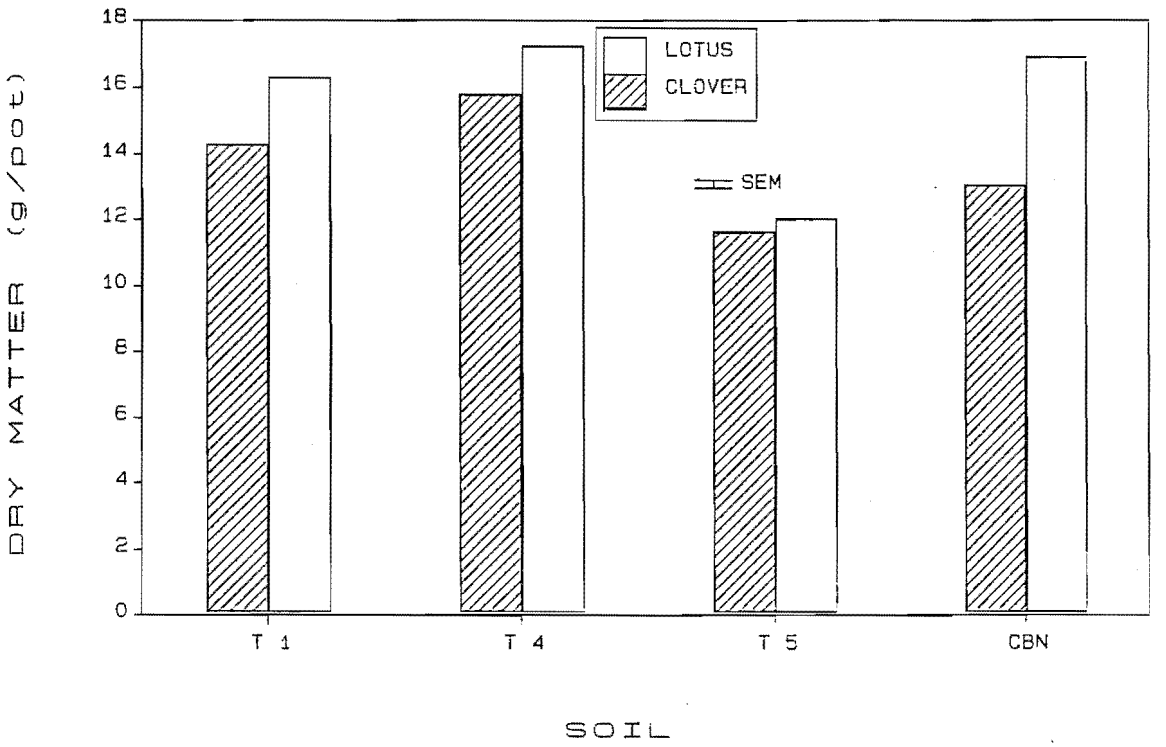


Figure 8.7 : The interaction between legumes and soil (Shoot DM (g))

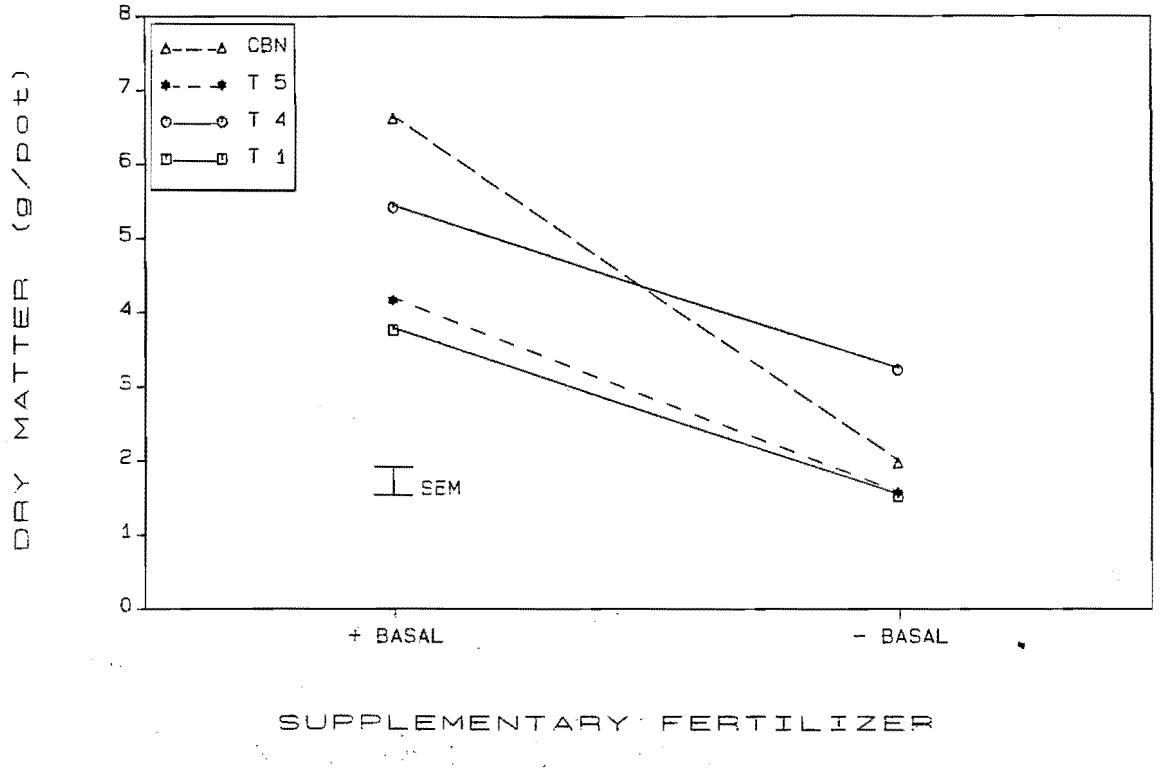


Figure 8.8 : The interaction between basal fertilisers and soil with Root DM (g)

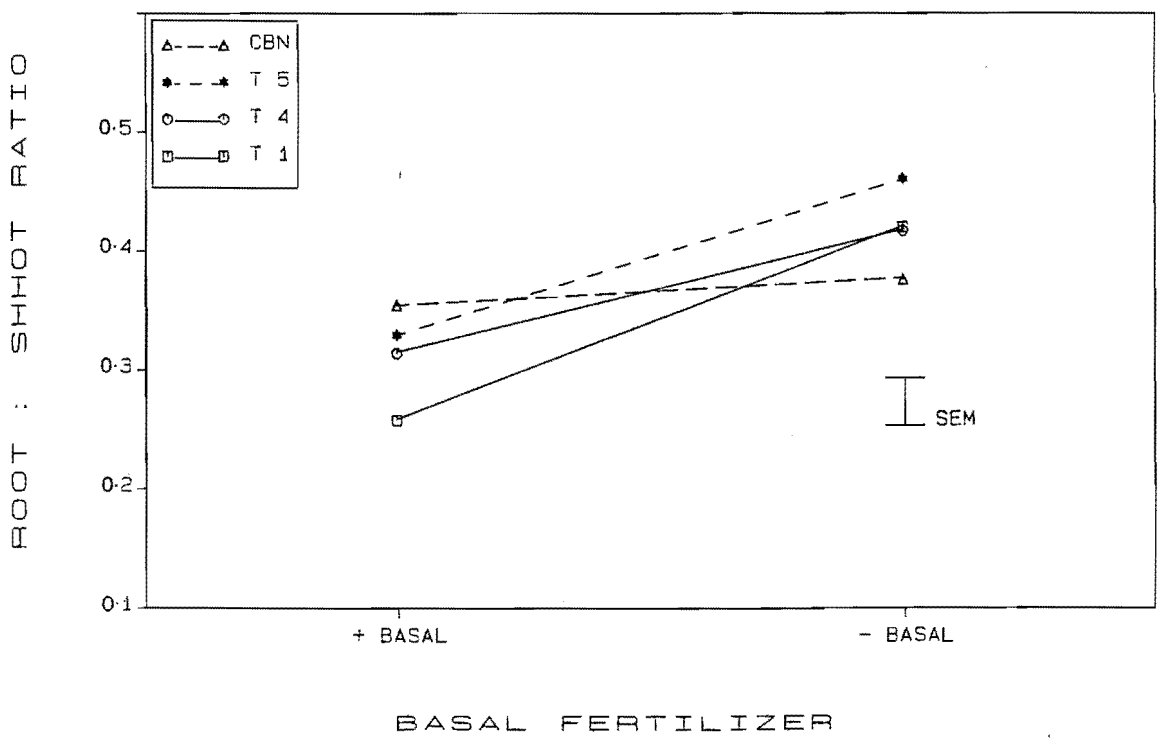


Figure 8.9 : The interaction of basal fertiliser and soils with legume root: shoot ratio

basal by soil interaction was due to the high Craigieburn R:S ratio without basal and on T1 with basal (Fig. 8.9). Root: shoot ratios were higher on every soil with basal ($p < .001$)(Fig. 8.9).

8.3.2 Mineral Content

(a) Shoot and Root N and P Concentration and uptake

Phosphorus, as expected, had the greatest treatment effect on shoot mineral concentrations and total uptake (Table 8.8).

Table 8.8: Effect of Treatment on Shoot Nutrient Content (ANOVA % Sum of Squares).

	Phosphorus				Nitrogen			
	Conc.		Uptake		Conc.		Uptake	
Phosphate	80.4	***	95.5	***	46.2	***	96.0	***
Legume	1.8	***	0.0	NS	0.3	NS	0.5	***
Soil	4.8	***	1.5	***	2.7	*	1.2	***
Phos. x Leg.	0.4	NS	0.2	NS	4.1	**	0.4	**
Phos. x Soil	2.0	**	0.9	***	4.6	NS	1.2	***
P x L x S	0.5	NS	0.2	NS	1.7	NS	0.2	NS

Shoot P concentrations were higher on T1 and T5 than other soils ($p < .001$) with the greater P response between P_{25} and P_{100} on T_1 the main factor contributing to the significant soil by P interaction ($p < .001$; Fig. 8.10). Clover P concentrations were higher than lotus at every P level (Fig. 8.11; mean 1.65 vs 1.42 mg P g^{-1} DM). Shoot DM production in relation to shoot P concentration was similar in both legumes (Fig. 8.12).

Shoot N concentration increased slightly but significantly with increasing P rate ($p < .001$). The greater clover N concentrations at P_{400} and lower concentrations at P_{25} relative to lotus caused a significant P by legume interaction ($p < .007$; Fig. 8.13). N concentrations were significantly higher on T5 than other soils ($p < .046$; Table 8.9). No other treatment effects or interactions were significant.

Table 8.9: Shoot N concentration on Puffers and Craigieburn Soils. (mg N g^{-1} DM).

Legume	Soil					
	T1	T4	T5	CB4	MEAN	SEM
Lotus	23.0	23.5	24.8	24.7	**24.0**	0.3
Clover	24.8	23.5	25.3	24.4	**24.5**	
Mean	**23.9**	**23.5**	**25.1**	**24.4**		0.4

Total P uptake in shoots, increased directly with applied P ($p < .001$) with the higher uptake on T1 causing the soil by P interaction ($p < .001$; Fig. 8.14). The mean difference between legume uptake, 28.2 and 27.5 mg P pot^{-1} for clover and lotus respectively, was not significant. However lotus accumulated more P than clover at low P rates ($p < .09$; Fig. 8.15).

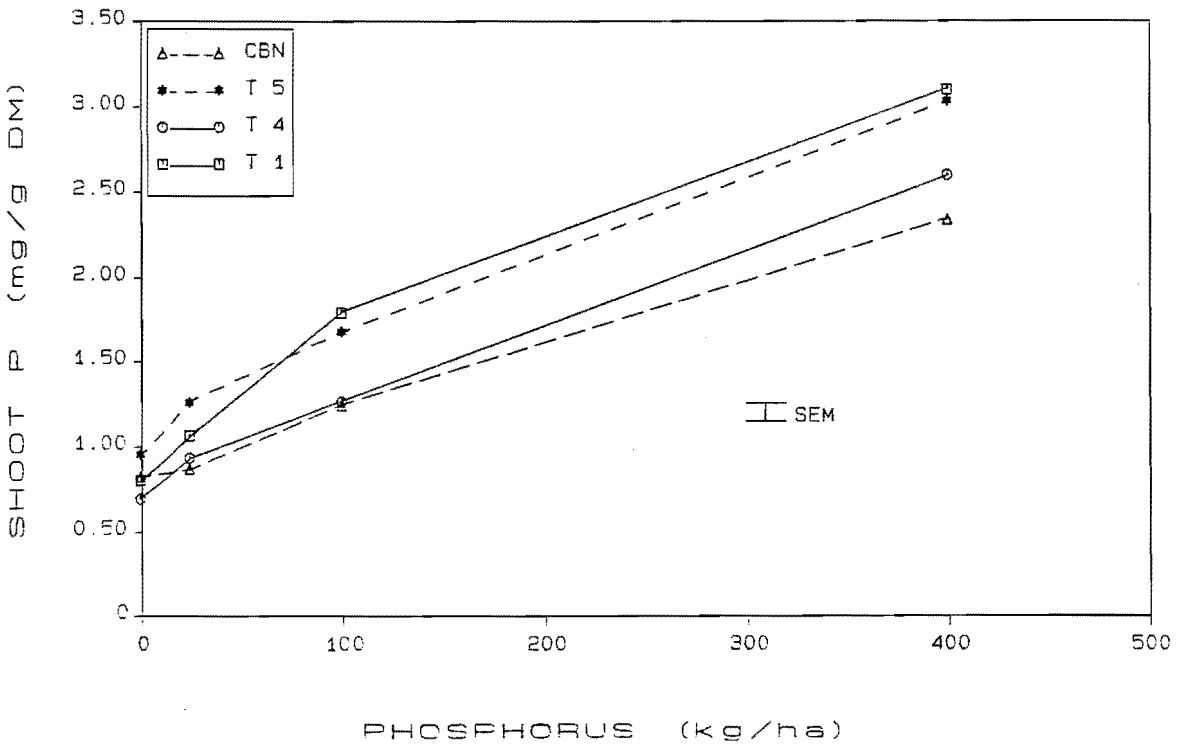


Figure 8.10 : The effect of applied P on shoot P concentration on soils T1-CB4

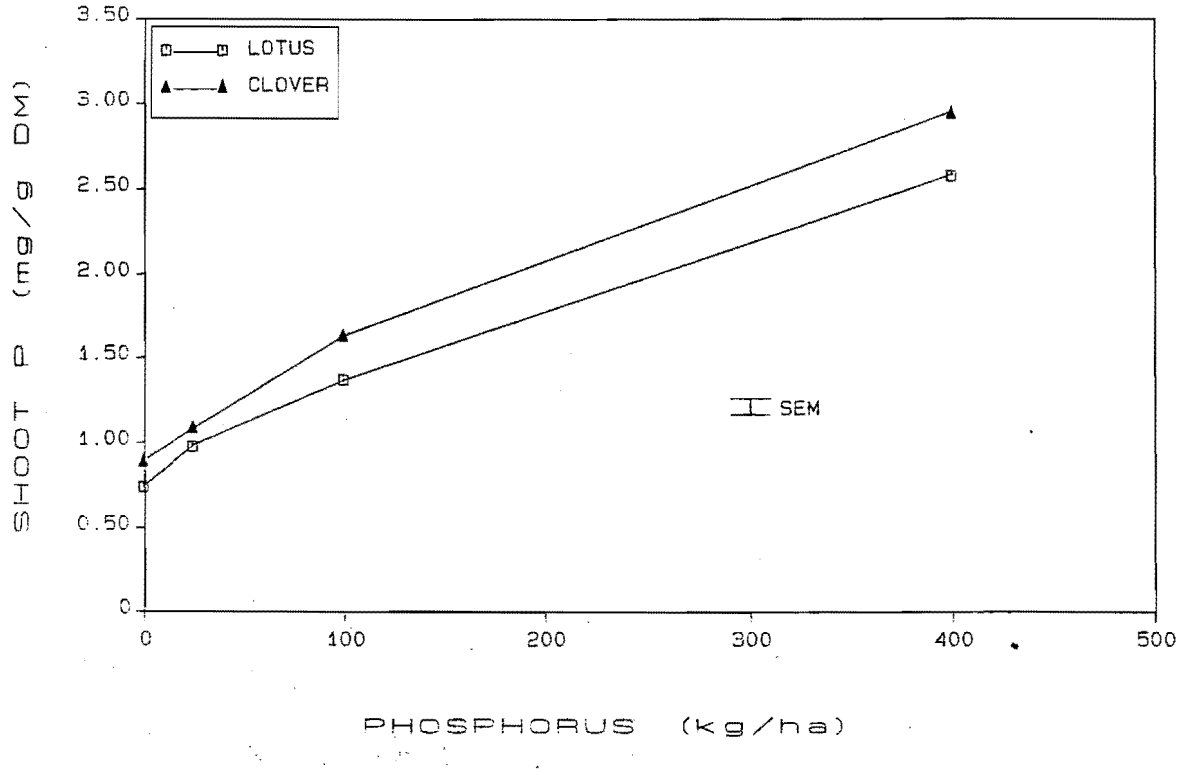


Figure 8.11 : The effect of applied P on lotus and clover shoot P concentration

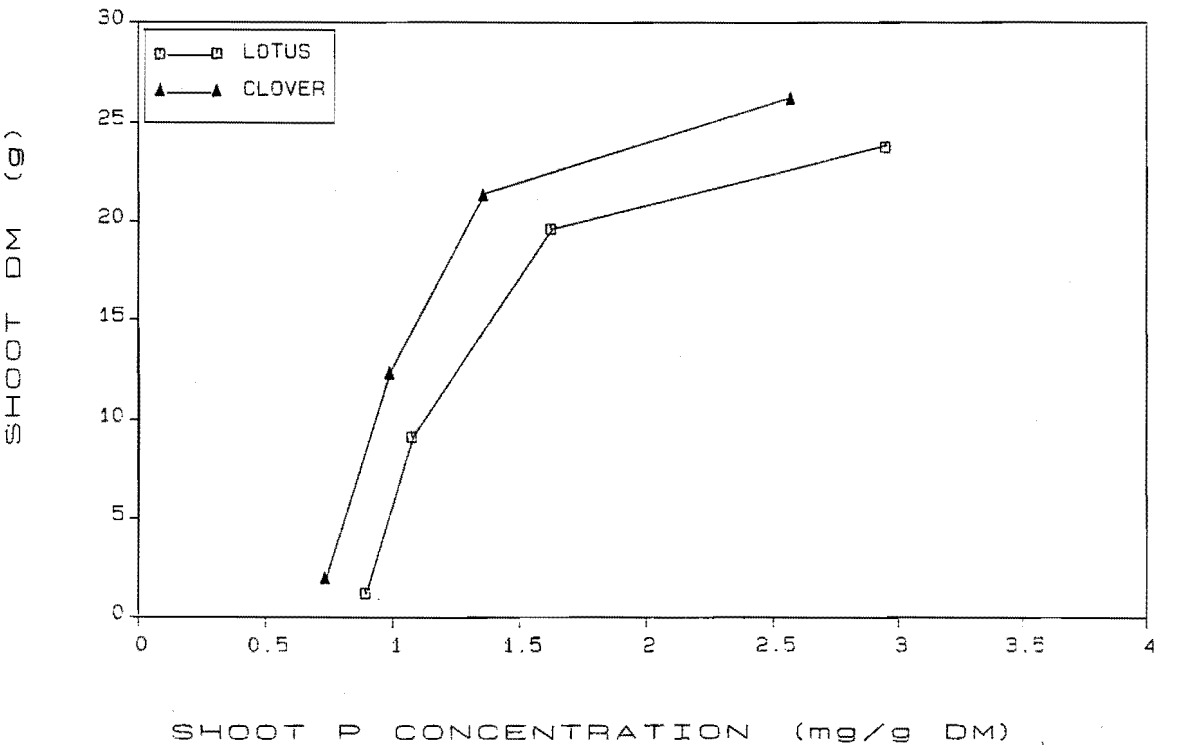


Figure 8.12 : Lotus and clover shoot DM production in relation to shoot P concentration

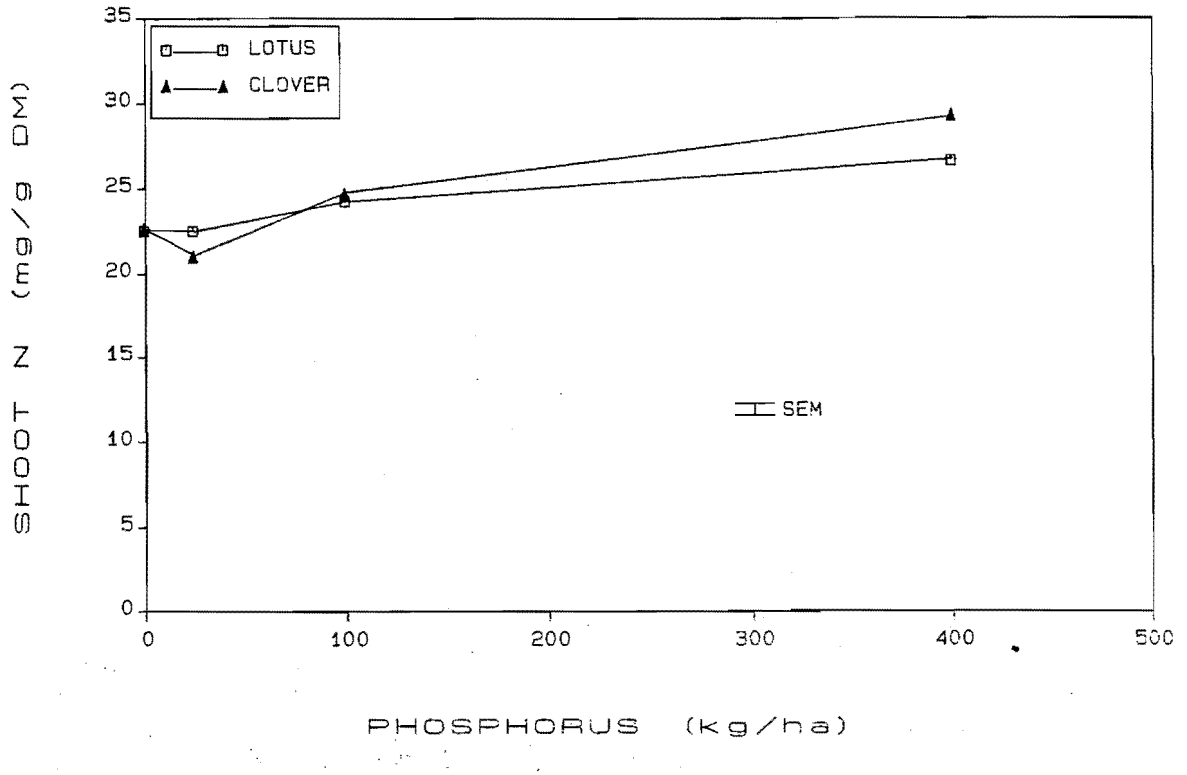


Figure 8.13 : The effect of applied P on lotus and clover shoot N concentration

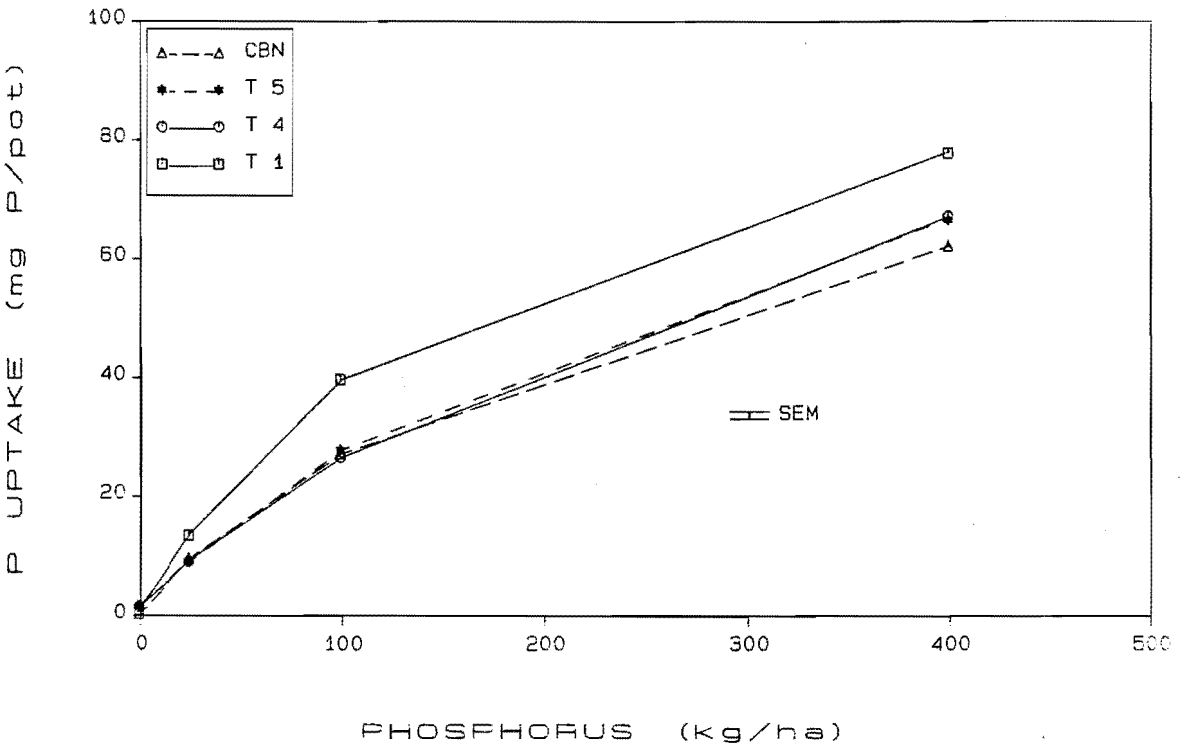


Figure 8.14 : The effect of applied P on shoot Total P uptake on T1-CB4

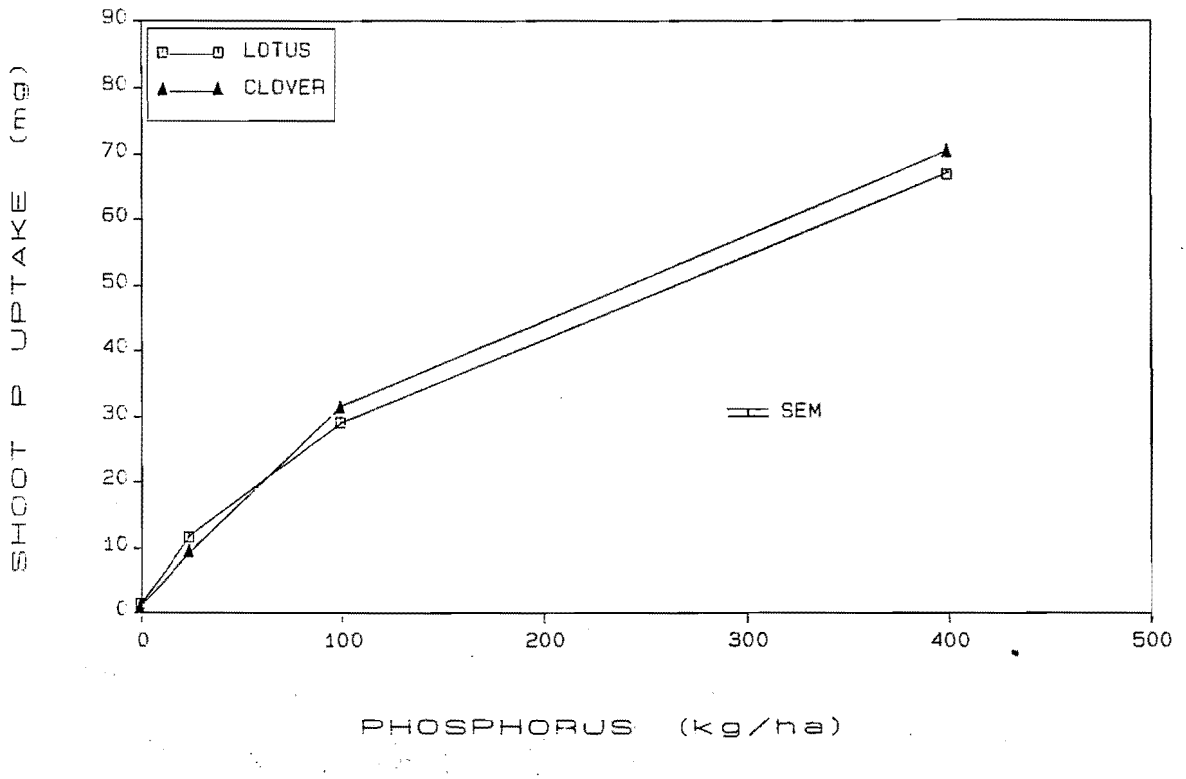


Figure 8.15 : The effect of applied P on lotus and clover shoot Total P uptake

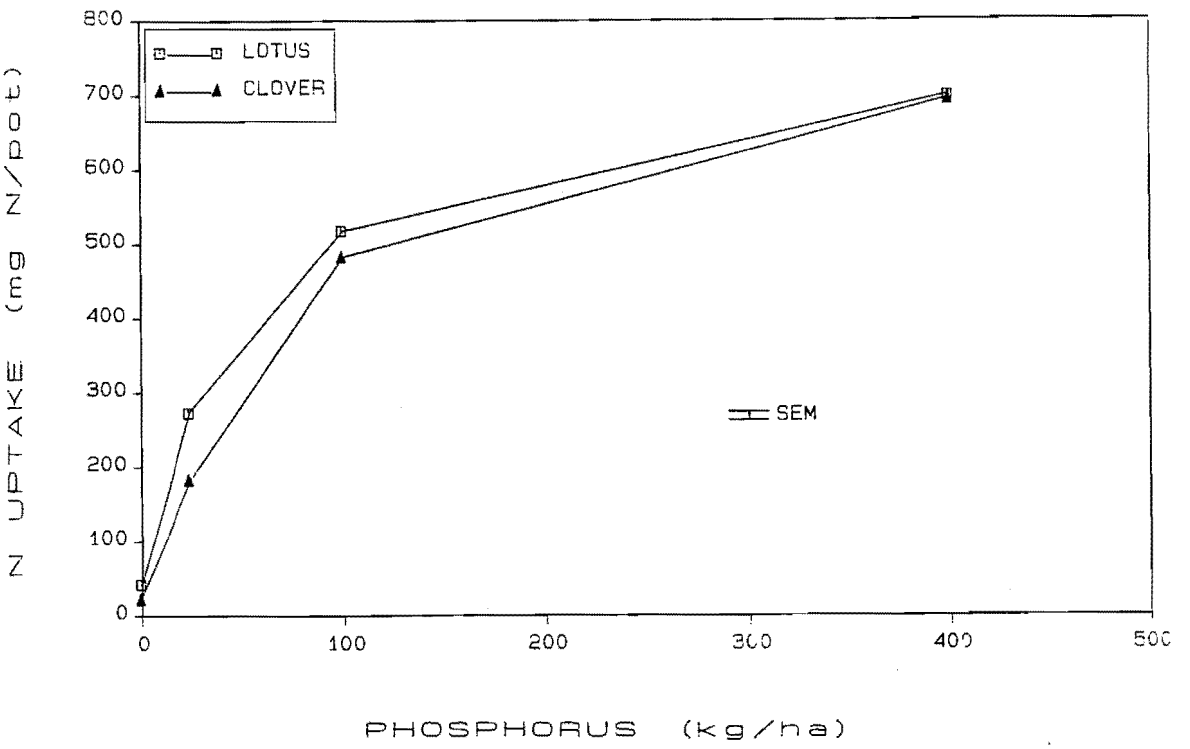


Figure 8.16 : The effect of applied P on lotus and clover shoot Total N uptake

Nitrogen uptake in shoots differed significantly between legumes with lotus outyielding clover (385 vs 348 mg N/pot). The greater lotus N yield at low P but not at high P rates, similar to P uptake, caused a significant P by legume interaction ($p < .004$; Fig. 8.16). Nitrogen uptake on soils differed ($p < .001$) with the lower increase in uptake on T1 above P_{100} relative to other soils resulting in a significant soil by P interaction ($p < .001$, Fig. 8.17).

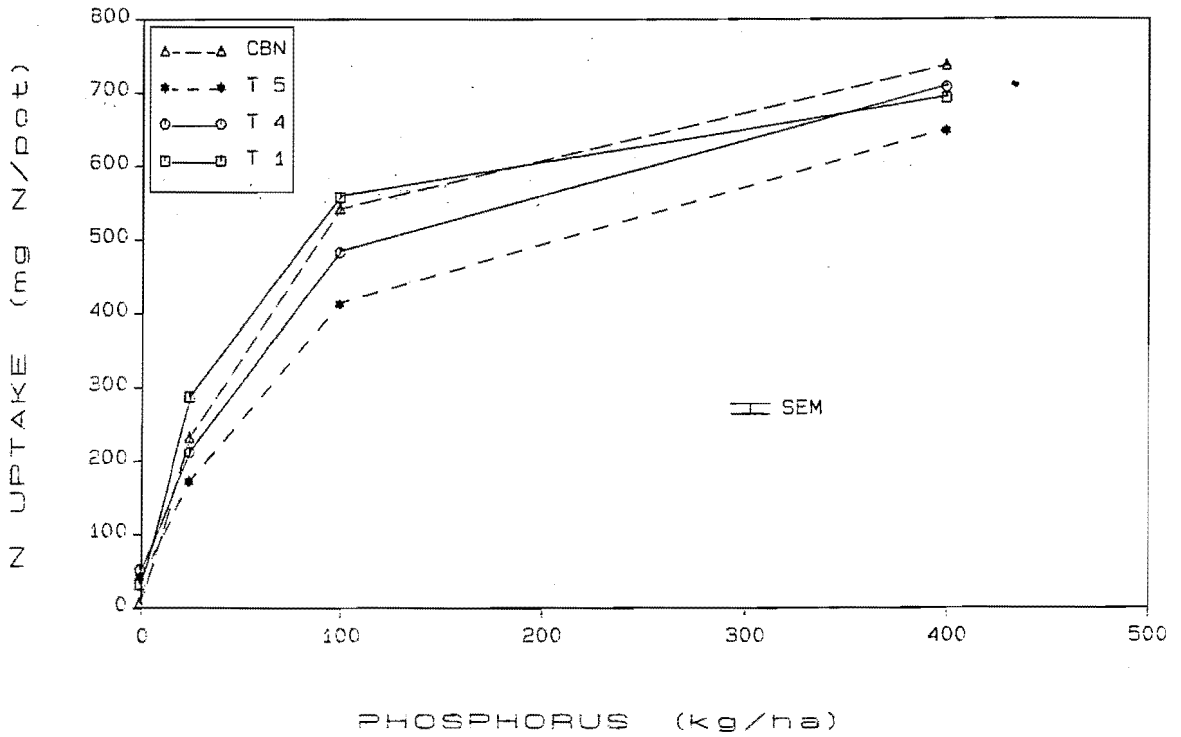


Figure 8.17 : The influence of applied P on shoot Total N uptake in soils T1-CB4

(b) Basal Fertiliser Effect

Effect of basal fertilizers on shoot mineral contents are summarised in Table 8.10.

Table 8.10: Effect of basal fertilizers on shoot nutrient content (ANOVA % sum of squares and significance).

	Phosphorus				Nitrogen			
	Conc.		Uptake		Conc.		Uptake	
Basal	54.6	***	29.3	***	12.3	**	72.8	***
Legume	4.1	***	0.0	NS	0.1	NS	1.4	*
Soil	21.9	***	16.0	***	2.9	NS	5.1	***
Basal x Leg.	0.4	NS	2.6	*	0.7	NS	0.1	NS
Basal x Soil	0.5	NS	8.7	**	15.7	**	5.7	***
Legume x Soil	0.5	NS	2.7	NS	2.6	NS	1.1	NS
Basal x L x S	1.6	NS	1.8	NS	2.2	NS	0.1	NS

Shoot P concentrations were higher in clover than lotus (1.94 vs 1.73 mg P g^{-1} DM; $p < .001$). P concentrations were always higher without basal ($p < .001$) with significant differences between soils ($p < .001$; Table 8.11).

Table 8.11: Effect of basal fertilizers on shoot P concentration on different soils (mg P g^{-1} DM).

Basal	Soil					
	T1	T4	T5	CB4	MEAN	SEM
+ Basal	1.78	1.25	1.65	1.23	**1.48**	0.04
- Basal	2.58	1.96	2.44	2.15	**2.28**	
Mean	**2.14**	**1.56**	**2.00**	**1.64**		0.05

Total P uptake in shoots was greater with basal (30.1 vs 20.1 mg P pot^{-1}; $p < .001$) with the greater decrease in uptake in clover without basal causing the P by legume interactions ($p < .05$, Fig. 8.18). P uptake was markedly higher on T1 relative to other soils with basal and lower on T5 and CB4 without it, causing the soil by basal interaction ($p < .01$; Table 8.12).

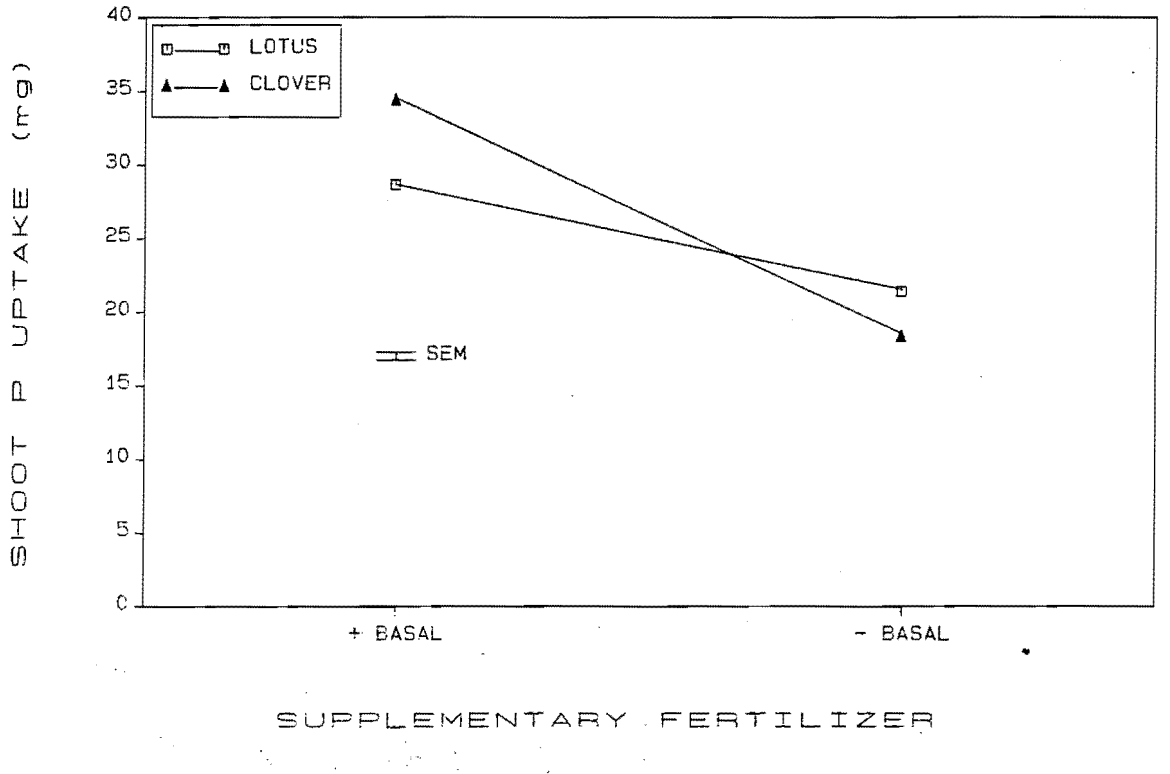


Figure 8.18 : The effect of basal fertilisers on lotus and clover Total P uptake

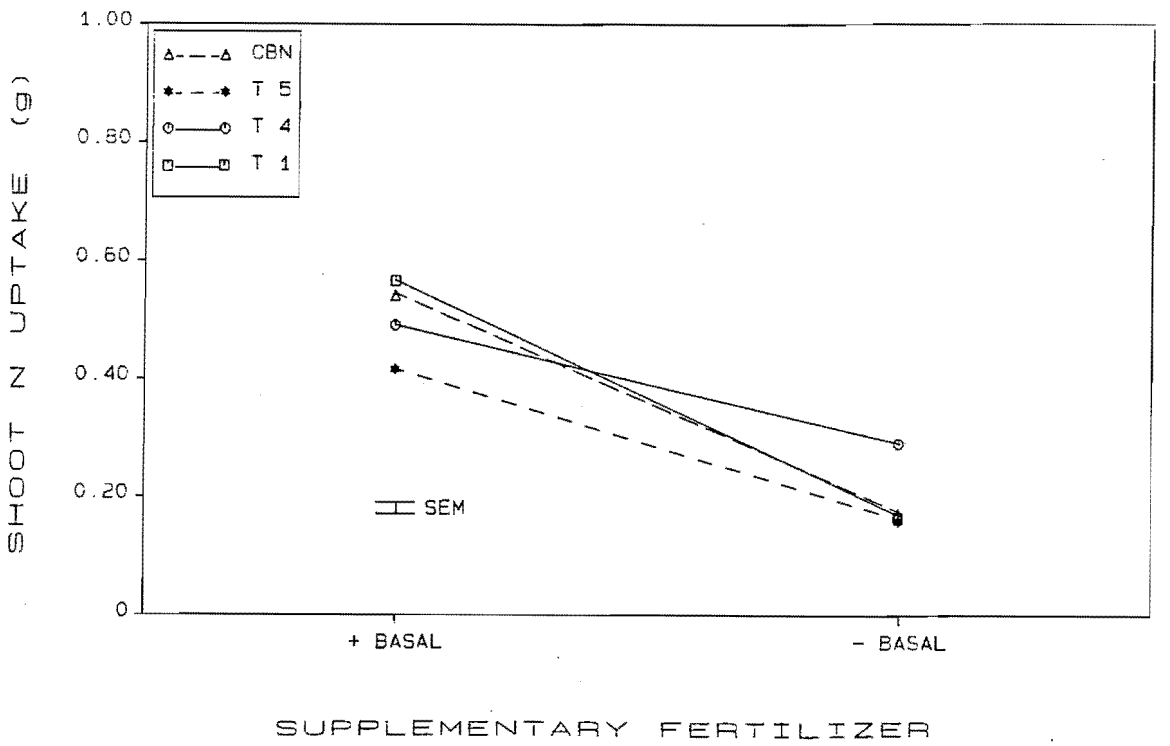


Figure 8.19 : The influence of basal fertilisers on shoot Total N uptake in soils T1-CB4

Table 8.12: Effect of Basal fertilizers on Shoot P uptake on different soils (mg P pot^{-1}).

Basal	Soil					
	T1	T4	T5	CB4	MEAN	SEM
+ BASAL	39.5	26.3	27.5	27.1	**30.1**	1.0
- BASAL	21.7	23.2	17.6	17.9	**20.1**	
Mean	**31.6**	**24.9**	**23.1**	**23.0**		2.0

Shoot N concentrations, in contrast to P, were higher with basal fertilizers than without ($p < .01$; Table 8.13). The only exception, occurred on T4 causing the soil by basal interaction ($p < .01$; Table 8.13). Differences between legumes and soils were not significant (Table 8.10).

Table 8.13: Effect of basal fertilisers on shoot N concentration on different soils (mg N/g DM).

Basal	Soil					
	T1	T4	T5	CB4	MEAN	SEM
+ Basal	25.3	23.2	25.3	24.9	**24.7**	0.4
- Basal	21.0	24.5	23.6	21.9	**22.7**	
Mean	**23.4**	**23.8**	**24.5**	**23.6**		0.6

Shoot uptake as a proportion of total N uptake was higher with basal fertilizers (0.51 g/pot) than without (0.20 g/pot; $p < .001$). Lotus N yield was higher than clover (0.39 vs 0.35 g N/pot; $p < .016$). The highly significant basal by soil interaction was due to the greater difference in N yield between basal treatment on T1 and Craigieburn soil relative to T4 and T5 ($p < .001$, Fig. 8.19).

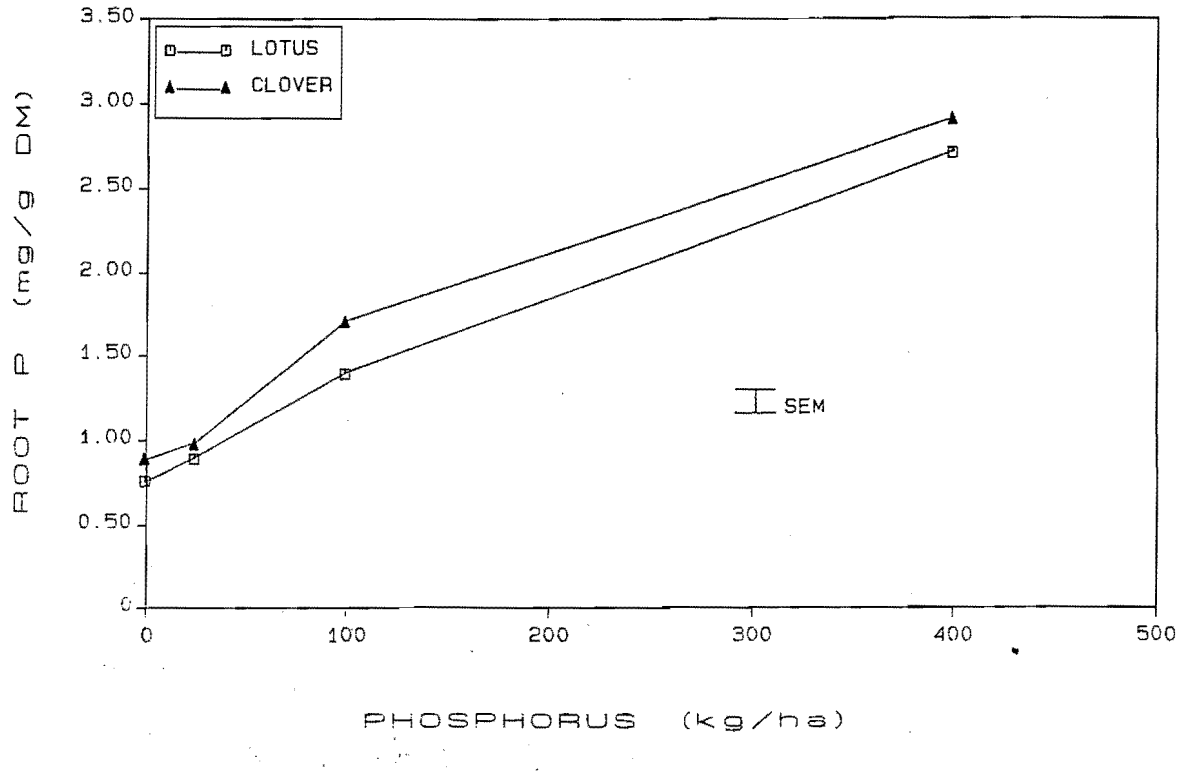


Figure 8.20 : The effect of applied P on lotus and clover root P concentration

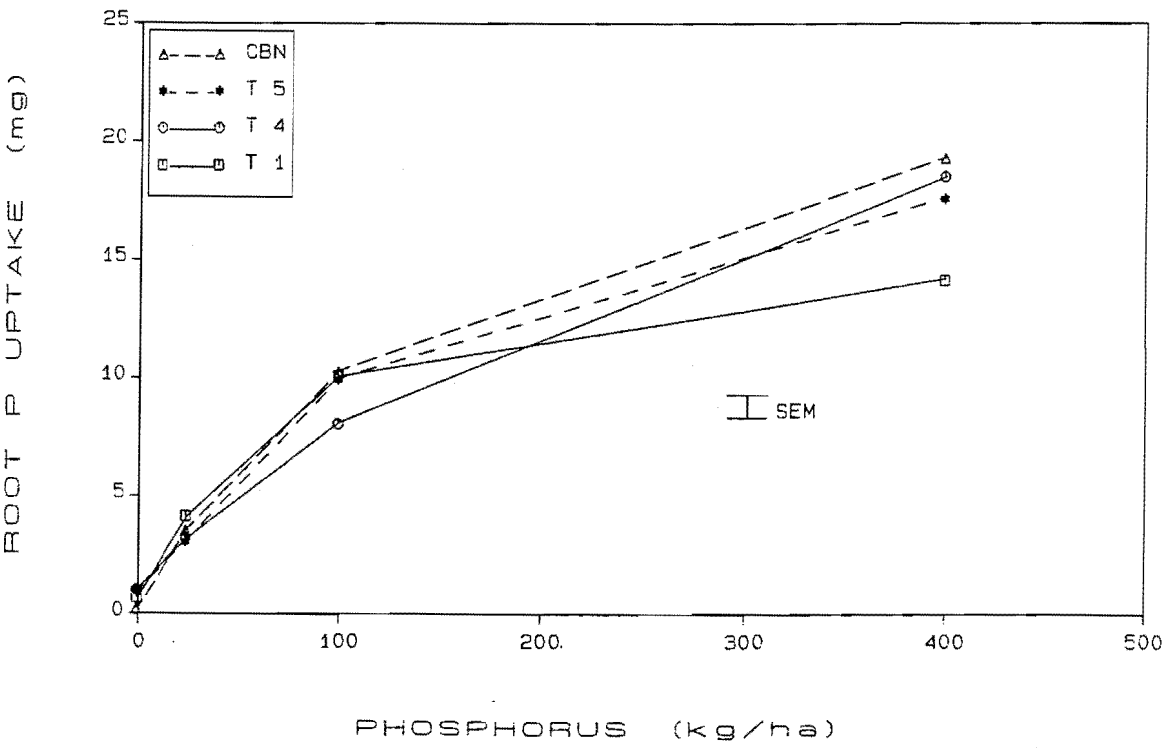


Figure 8.21 : The effect of applied P on root Total P uptake on T1-CB4

c) Root Mineral Content

Treatment effects on root mineral contents are summarized in Table 8.14.

Table 8.14: Effect of treatment on root mineral content. (ANOVA % sum of squares).

	Phosphorus				Nitrogen			
	Conc.		Uptake		Conc.		Uptake	
Phosphate	86.9	***	93.4	***	52.5	***	81.8	***
Legume	1.1	*	0.0	NS	2.8	NS	0.5	NS
Soil	3.1	**	0.4	NS	2.3	NS	6.6	***
P x Leg.	0.2	NS	0.1	NS	3.9	NS	1.0	NS
P x Soil	2.1	NS	2.4	*	10.5	NS	7.0	**
Leg. x Soil	0.3	NS	0.1	NS	5.5	NS	1.9	*
P x L x S	0.5	NS	0.2	NS	8.0	NS	2.3	NS

Clover, as with shoots, maintained higher P tissue concentrations at all levels of applied P ($p < .02$). P concentrations in both species increased in almost direct proportion to applied P, similar to shoot P concentrations, and showed little rate of decrease even at P_{400} ($p < .001$; Fig. 8.20). Tissue concentrations were highest on T1 and T5 and lowest on Craigieburn and T4 ($p < .004$, Table 8.15).

Table 8.15: Root P concentration on different soil (mg P g^{-1} DM).

	T1	T4	T5	CB4	MEAN	SEM
Clover	1.75	1.44	1.83	1.50	**1.63**	0.52
Lotus	1.64	1.37	1.53	1.25	**1.45**	
Mean	**1.70**	**1.41**	**1.68**	**1.37**		0.73

Total root P uptake increased with applied P in all soils ($p < .001$) but the greater increase of P uptake in the Craigieburn soil between P_0 and P_{100} relative to other soils, and the comparatively small increase in T1 between P_{100} and P_{400} caused the significant soil by P interaction ($p < .039$; Fig. 8.21). Differences in uptake between legumes were not significant (Table 8.14).

Clover also maintained higher root tissue N concentrations than lotus ($p < .06$) particularly at high P levels ($p < .001$; Fig. 8.22).

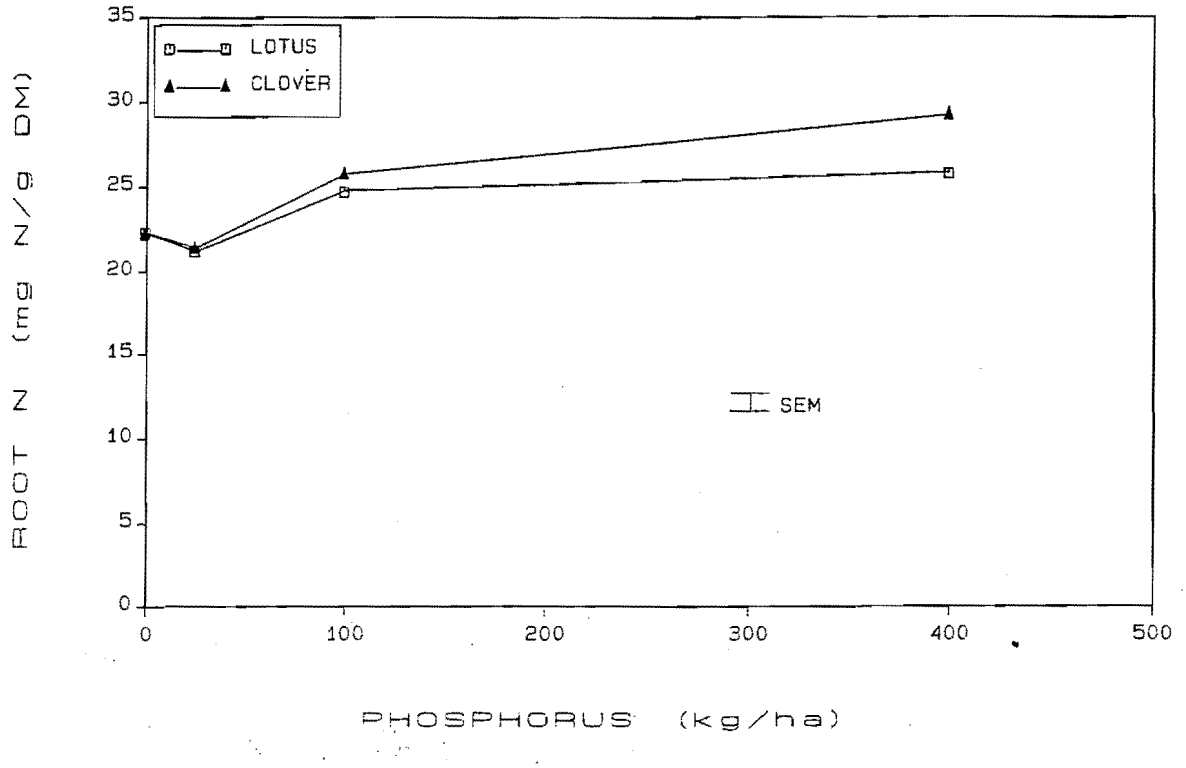


Figure 8.22 : The effect of applied P on root N concentration

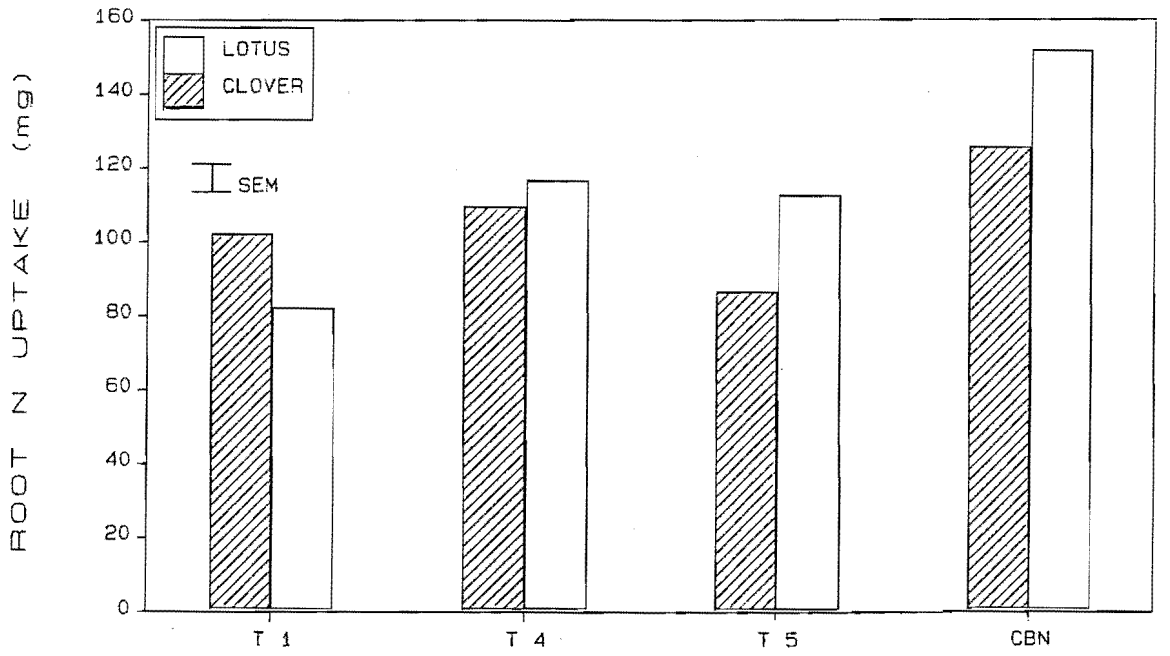


Figure 8.23 : Lotus and clover total root N uptake on T1-CB4

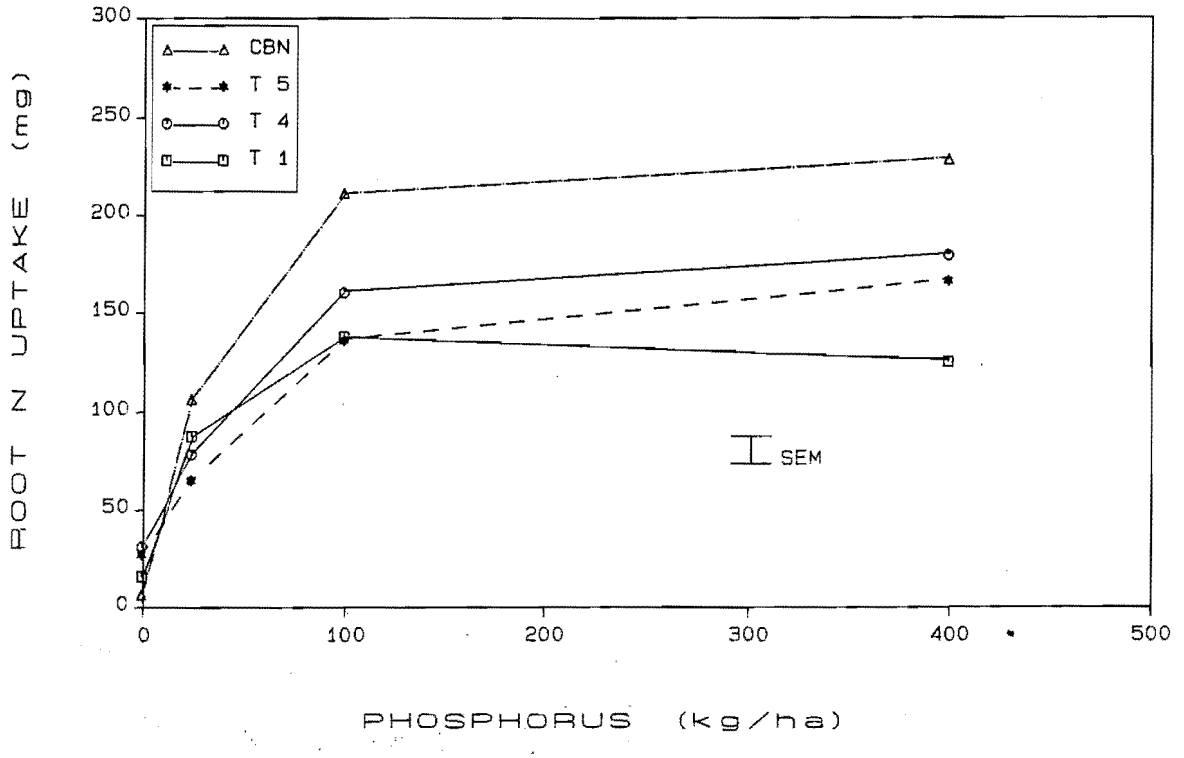


Figure 8.24 : The effect of applied P on root total N uptake on T1-CB4

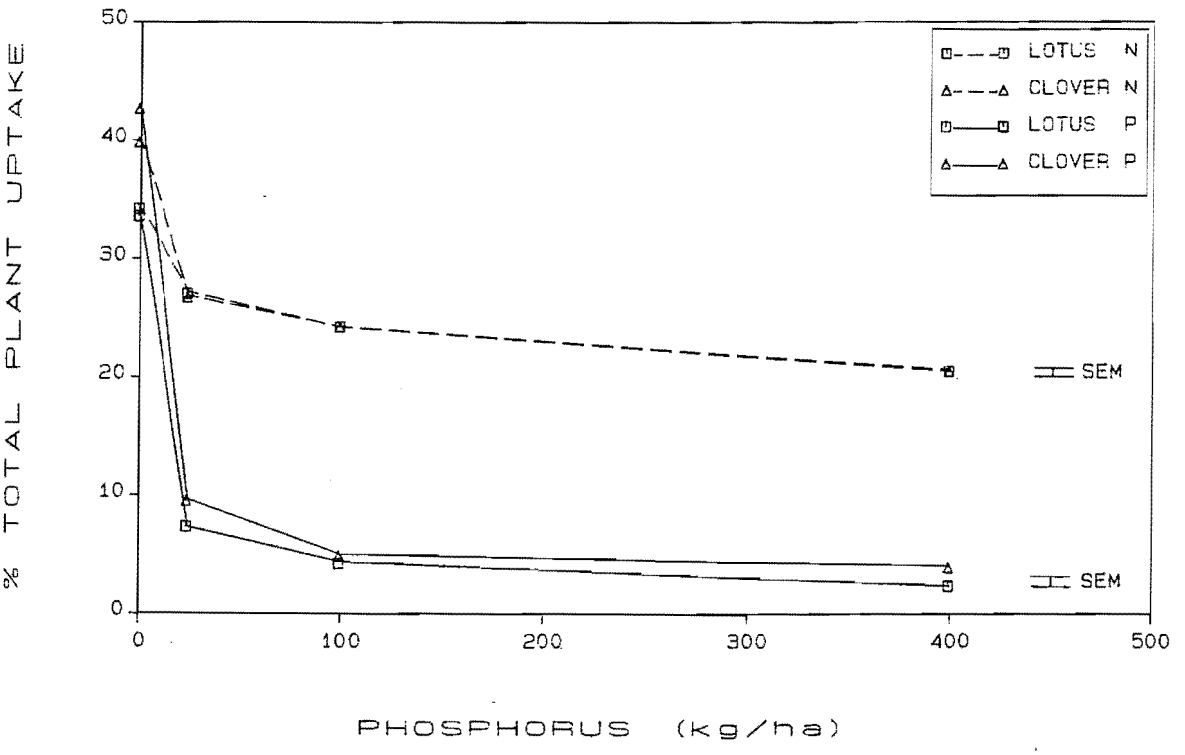


Figure 8.25 : The effect of applied P on the proportion of total N and P retained in lotus and clover roots

Total N uptake in roots differed between legumes depending on soil ($p < .041$). Clover N content was greater than lotus on T1, similar on T_4 and markedly lower on T5 and Craigieburn (Fig. 8.23). The soil by P interaction was highly significant ($p < .002$) and was due to the greater increase in N uptake in Craigieburn soils between P_0 and P_{25} relative to other soils and the decrease in uptake on T1 between P_{100} and P_{400} compared with slight increases on other soils (Fig. 8.24).

The percentage of total plant N and P retained in the roots was markedly greater at P_0 for both species ($p < .001$; Fig. 8.25).

8.4 DISCUSSION

8.4.1 Dry Matter Production

(a) Shoot and Root Yield

The rapid initial increase in DM production with applied P, then the slower rate of increase with further levels of applied P for both root and shoots (Figs. 8.1, 8.3) confirm the gross P deficiency of all four soils (New Zealand Soil Bureau 1968). However the numerous soil by P and legume by P interactions (eg. Figs. 8.1, 8.3, 8.5, 8.6 8.8, 8.14, 8.17, 8.18, 8.20, 8.24) show plant production to be determined by a complex interaction of edaphic factors not merely a simple P response.

Exchangeable aluminium was negatively correlated with both clover and lotus shoot DM (Table 8.5). Soil acidity, P retention, total P and cation availability were also highly correlated, though less strongly than exchangeable Al (Table 8.5). Exchangeable Al levels above 1.0 milliequivalents percent (me%) were considered toxic to Al sensitive species by Pratt (1966). Exchangeable Al levels were 1.7 me% in T5 and 1.0 me% in the Craigieburn soil, nine and five times greater respectively than in the T1 soil. The effects of Al toxicity and P deficiency are difficult to separate as increased P levels in soil solution can precipitate and detoxify Al as well as ameliorating P deficiency. (Foy 1974). Davis (1981a) in a pot trial with Bealey subsoil, demonstrated that applied P reduced soluble Al levels in the surface horizon. Thus part of the yield response observed in figure 8.1 may be due to alleviation of Al toxicity. This is the most probable explanation for the consistently lower P responses on T5 (Fig. 8.1). The depressed P response curve on T5 (Fig. 8.1) is a classic example of where a secondary factor limits the full response to P (Bouma 1983).

Al toxicity in adjacent Bealy and Katrine podzolized high country yellow brown earths has been demonstrated in pot trial to depress DM production of both legumes (Ali, 1974, Davis 1981 a,b,c, Haynes & Ludecke 1981a,b). Lotus was far more tolerant of Al than clover but still responded when lime depressed exchangeable Al levels. Soil acidity is generally considered a major factor determining the relative performance of the two legumes in field trials (During *et al.* 1964, Lambert *et al.* 1974, Lowther 1977).

(b) Field and Glasshouse Comparison

Comparison of soil DM production from the field trial with production in the glasshouse confirms field results (Table 8.6). The T1 yields in the glasshouse, being ten times greater in the field, provide strong evidence for the conclusion that soil moisture deficits, rather than soil fertility, limited field production (Chapter 6.4). The lower yields on T5 relative to T4 in the field (0.6 vs 1.0 relative to yield on T4) was confirmed in the glasshouse, though the actual difference between soils narrowed (0.6 to 0.8 relative to yield on T4; Table 8.6)). It seems reasonable to assume that observed differences in yield on other soils in the field trial, T2 and T3, are also principally due to edaphic rather than microclimatic differences.

Despite differences in trial duration, the same pattern held for the difference between field and glasshouse results for soils at the two study sites (Table 8.6). Thus the difference in relative lotus performance between Craigieburn field and glasshouse results was also 0.2 (0.8 field vs 1.0 glasshouse relative yield). The difference with clover was wider (0.6 vs 1.0 relative yield). These results support the comparison of the Craigieburn and Puffers Stream field data and again suggest the primary causative factor if edaphic. The differences between field and glasshouse results (between 0.2 to 0.4 relative to yield on T4) are reasonably similar, though slightly lower in magnitude, to the observed difference of 0.5 relative yield between sieved and intact soils in the soil structure experiment (Chapter 7).

The identical production ratio from Puffers Creek and Craigieburn structure experiment sieved soils with the pot trial (1.0 vs 1.03 in both experiments, Table 8.6) demonstrate for lotus that pot depth, presense of sub soil horizons and soil volume appear of little effect for short term experiments with high levels of surface applied nutrients. This agrees with Davis' (1981a) observation that applied P stayed within 0-2 cm of the pot surface in short term pot trials.

Lotus outyielded clover in the glasshouse in striking contrast to second season herbage yields in the field (Chapter 6.3.3) where the reverse occurred. Shoot and root production in the glasshouse were greater than clover at all P rates, particularly at low P, (Figs. 8.2, 8.3). The superior lotus performance at levels of low P availability has been widely demonstrated in pot, field and solution culture experiments (Nordmeyer & Davis 1977, Caradus 1980, Kee 1981, Lucas *et al.* 1981, Scott & Mills 1961, Hart 1981, Haynes & Ludecke 1981b). Results differed as to which legume produced most at high P levels. Results from this study, where lotus outyielded clover even at P_{400}, agree with Bealy subsoil experiments (Davis 1981a,b), Egmont Subsoil (Hart & Jessop 1983) and Mesopotamia field trial results (Lucas *et al.* 1981) but contrast those of Haynes & Ludecke (1981b), Hart *et al.* (1981b) and Brock (1973) on less acidic or heavily limed soils.

The decrease in root:shoot ratio as P levels increase (Fig. 8.5) plus the parallel decrease in total P retained in the root (Fig. 8.25) is strong evidence for P deficiency. The strategy of allocating an increased proportion of plant resources to roots in and attempt to overcome nutrient deficiency is well established (Shank 1945, Brouwer 1962a,b, Biddiscome *et al.* 1969, Davidson 1969, Osanne *et al.* 1969, Atkinson 1973, Brock & Hoglund 1974, Whittaker *et al.* 1976, Hart *et al.* 1981b, Mouat 1983). Similarly, when a nutrient is limiting roots often transport a lower proportion of the absorbed nutrient to shoots then when supply

is adequate (Moorby & Besford, 1983). This is consistant with the highest root:shoot ratios occurring in the Craigieburn soil with high P retention capability (Table 8.4) and therefore the most intense soil competition for applied P. The lowest ratios occurred on T5, with the second lowest P retention and T1, the most fertile soil with the lowest P retention (Table 8.4).

(c) Basal Fertilizer Effect

The sharp decline in yield with high applied P but no basal fertilizer demonstrates secondary nutrient limitations. (Figs. 8.6 and 8.8). The very low topsoil sulphate (SO_4) values (Table 8.4) suggest sulphur deficiency. Sulphur deficiency is widespread in high country yellow brown earths (O'Connor 1962, N.Z. Soil Bureau 1968, Ludecke & Leamy 1972, McLeod 1974, Douglas & Kinder 1975, Douglas & Risk 1981, McIntosh *et al.* 1984, 1985). O'Connor (1961c) has shown the Craigieburn soil to be deficient in sulphur. Furthermore, on five upland or podzolised yellow-brown earths P responses for both clover and lotus were consistently far higher when 50 kg S ha^{-1} was applied with P, compared with P alone (McIntosh *et al.* 1984). Since McIntosh's topsoil SO_4 indices were twice those in this study it is highly probable that S deficiency, either alone or in part, is primarily responsible for the yield depression without basal fertiliser.

The high correlation coefficients of yield with cation exchange capacity, base saturation percentage and magnesium (Table 8.5) mean the possibility of a cation deficiency cannot entirely be ruled out. The higher shoot and root yield on T4, and the proportionally lower reduction in yield without basal relative to other soils (Fig. 8.6) may indicate Mg or K deficiency since these elements are markedly higher in T4 than the other soils (Table 8.4). If so, then the large reduction in CB4 shoot and root production without basal (Figs. 8.6 and 8.8) suggests that Mg may be in greater deficiency since K levels are quite high on this soil (Table 8.4). Likewise calcium does not appear responsible since T1 shoot yield was equally reduced by basal omission as CB4, despite T1 having the highest Ca concentration of all the soils (Table 8.4; Fig. 8.6).

8.4.2 Mineral Content

(a) Shoot & Root Contents

Shoot and root P concentration continued to directly increase with applied P in both species with no apparent plateaux (Figs. 8.11, 8.20). The inverse relationship between rate of shoot DM accumulation per unit of applied P (Fig. 8.1) resulted in 81.5 and 82.4% of the maximum production attained in this experiment for clover and lotus at shoot P concentrations of 1.7 and 1.4 mg P g^{-1} DM respectively (Fig. 8.12). This shows near-maximum production is occurring well below the suggested critical P concentration for clover between 0.30 - 0.40%P (McNaught, 1970) and 0.25-0.30% P for lotus (Kee 1981). Precise determination of critical P concentrations are not possible from this experiment as

the response curves (Fig. 8.12) are incomplete. Nevertheless the curves do suggest the critical concentrations are probably close to the lower limits of the suggested range i.e. 0.25% P for lotus and 0.30 %P for clover.

The lower lotus shoot and root P concentration and higher DM production per unit applied P indicate it is more efficient (Blair and Cordero 1978) in the use of absorbed P and more efficient in recovering applied P than clover (Figs. 8.11 and 8.20). This agrees with previous pot trials (Hart 1981, Davis 1981a, 1981b, 1981c, Haynes and Ludecke 1981a, 1981b, Hart & Jessop 1983) and field trial results (Brock 1973, Gibson *et al.* 1975, Lowther 1980, Scott & Lowther 1980, Kee 1981). However the similar behaviour of lotus to clover, in continuing to increase tissue P concentrations at high P supply (Fig. 8.11) while growth only increased marginally (Fig. 8.2) is different from the relatively small increase in lotus shoot P concentration at high P supply found by Davis (1981b), Hart *et al.* (1981a) and Hart & Jessop (1983). The strategy of resource capture, as lotus demonstrated in this experiment, is typical of plants adapted to fertile soil (Chapin 1980).

Differences in shoot and root mineral composition and uptake demonstrate differences in nutrient supplying power of the four soils. The higher shoot and root P concentration in T1 and T5 is due to the greater availability of applied P on these soils. They have the lowest P retention and thus less soil competition for applied P. Conversely, CB4, with the highest P retention had the lowest tissue P concentrations and slightly lower P uptake (Figs. 8.10 and 8.14). The high P concentration in T5 shoots (Fig. 8.10) is because there was less growth (Fig. 8.1) and hence less growth dilution on this soil.

Total shoot P uptake differentiates T1 from all the other soils which did not differ significantly in P uptake (Fig. 8.14). The similarity of T5 uptake with CB4 and T4 shows availability of P is not solely responsible for the lower DM production on this soil. Root P uptake (Fig. 8.20) is very similar to shoot P uptake (Fig. 8.10) except for the lower uptake at P_{100} on T4 and the very small increase in T1 root P between P_{100} and P_{400}. The T1 result may be due to factors associated with restricted root volume as, having a higher sand content than the other soils and therefore a higher bulk density, there was less root volume available per pot for the same weight of soil compared with other soils (the soil surface was 3-4 cm lower than in other pots). T1 shoot DM leveled out at P_{400} (Fig. 8.1) reducing shoot demand for P and presumably root uptake.

Nitrogen concentrations in shoot and root tissue, in a similar pattern to P concentrations, were higher in clover than lotus at all P rates (Figs. 8.13 and 8.22). The only significant exception was shoot N at P_{25}. This decrease in N concentration from P_0 is almost certainly due to increased growth once the P deficiency was amended. At P_0 growth was minimal (Figs. 8.1, 8.3), soil N supply moderate (Table 8.4) and therefore tissue N concentrations were high as surplus N accumulated. With $P_{12.5}$ addition, sufficient P was available to stimulate growth, lowering N concentrations by growth dilution. As P levels rose further, DM accumulation peaked, and N fixation was sufficient to provide sufficient N to increase tissue concentrations. Increased N fixation and N content has been shown to increase with rate of applied P (Brock 1973). The drop in shoot N concentration between P_0 and P_{25} is clearly seen in Fig. 8.13. The ability of lotus, via rhizobia, to maintain shoot

N supply at a higher level than clover under low P conditions may provide it with a competitive advantage in these situations.

Total N uptake in lotus was greater than clover in both shoot and roots (Figs. 8.16, 8.23). Shoot N uptake was greater at lower P levels, the difference narrowing at P_{400}. These higher lotus total N and P yields agree with results from other workers (eg. Brock 1973, Davis 1981a, Hart and Jessop 1983).

Comparing the total shoot N uptake in soils (Fig. 8.17), the lower uptake in T5 relative to other soils is probably due to lower growth, as discussed for P. The high tissue N concentrations in T5 (Table 8.9) argue against the low N uptake being attributed to N limitation. The lower clover N uptake on T5 and CB4 relative to lotus (Fig. 8.23) suggests, as is well known (Norris 1956) that lotus rhizobia are more tolerant of acidity. This ability to obtain N under acid conditions gives lotus a comparative advantage over clover.

A similar pattern occurred with root N uptake though, in contrast to shoots, N uptake did not increase markedly in any soil except T5 above P_{100} and it decreased in T1 (Fig. 8.24). Why CB4 uptake is higher than other soils at all P levels greater than P_{25} is also not clear. Soil N levels were highest in the Craigieburn soil (Table 8.4) so possibly enhanced mineral N supply is responsible. Alternatively the physical structure of the Craigieburn soil, its lower bulk density and higher porosity, may favour N fixation.

(b) Basal Fertilizer Effect

Shoot P concentrations were higher without basal fertilizers due to P accumulation from the high rate of applied P and lower DM production. Conversely the higher shoot N concentration and total N uptake with basal fertilizers show basal increased plant available N, presumably through a direct effect on rhizobial N fixation.

The greater depression in P uptake in clover without basal relative to lotus (Fig. 8.18) again demonstrates lotus's superior ability to extract P from soil under low nutrient availability. This difference between legumes also suggests clover has a greater requirement for sulphur, molybdenum or basal cations for its P nutrition.

Shoot total N uptake was least affected on T4 by absence of basal fertilizer (Fig. 8.19) with the greatest reduction occurring on Craigieburn at T1. This again suggest cation deficiency may be responsible, as discussed for DM yield.

8.5 CONCLUSION

This glasshouse experiment showed four Craigieburn high country and related yellow-brown earth topsoils to have a major effect on legume yield. This provides strong evidence for edaphic causation of the observed differences in field experiments, particularly between study sites. Glasshouse herbage ranking between soils was, excepting T1, similar to ranking in the field experiment. The high production on T1 in the glasshouse demonstrated that the low yield in the field were not due to topsoil infertility. The similar relative performance between T4 and CB4 in glasshouse pot and large core experiments showed that for pot trials, running for up to 15 weeks, with high levels of surface applied nutrients and adequate water, pot volume or subsoil appear to have little affect on yield.

The four topsoils were grossly phosphorus deficient, almost certainly sulphur deficient and possibly marginal in cation supply for legumes. Clover and lotus herbage yields both decreased as topsoil exchangeable aluminium levels increased. Clover yield was depressed more than lotus. Aluminium toxicicity is probably directly responsible for the depression. Part of the legume response to applied P is probably due to amelioration of exchangeable aluminium. Legume P uptake decreased as soil P retention increased. Legume P response, therefore, increased with the degree of pedological development in these soils.

Lotus root and shoot production exceeded clover, particularly at low P levels. Lotus yield was also reduced less without basal fertilisers. Clover shoot and root N and P concentrations were consistantly higher than lotus though total plant uptake was generally less than lotus. The differences in uptake were greatest at low P levels, without basal fertiliser, or on soils with high exchangeable Al or acidity. Lotus therefore appears more efficient at extracting P from infertile soils than clover with a greater efficiency of herbage production per unit applied P.

Lotus rhizobia are inferred, from the higher lotus N content, to be superior to clover rhizobia under low P levels, without basal fertiliser and higher soil acidity. Ability to obtain N is probably also a significant factor in the superior lotus performance relative to clover under such conditions.

These results are consistant with lotus being adapted to lower fertility soils than clover and therefore edaphically more suited to HC YBE soils than clover. They support the working hypothesis that:

'lotus herbage production will be greater than clover, and that the relative difference in yield will be inversely related to P availability and will increase with soil pedological development'.

GENERAL DISCUSSION

GENERAL DISCUSSION

Contents

9.1 Preamble

The aim of this study was to investigate the edaphic ecology of selected indigenous and agronomic species on Craigieburn high country yellow brown earth and related soils.

The indigenous species, fescue tussock (*Festuca novae-zelandiae*) and matagouri (*Discaria toumatou*) are two of the physiognomically most important species in the montane eastern South Island tussock grasslands (Chapters 1.5, 2.1). Lotus (*Lotus pedunculatus* cv 'Grasslands Maku') and clover (*Trifolium repens* cv 'Grasslands Huia') are two legumes with high potential for pastoral development of these grasslands (Chapter 6.1).

Two soil development sequences, Puffers Stream (594m a.s.l. ; 905 mm mean annual precipitation) with soils T1-T5, and Craigieburn (793m a.s.l. ; 1470 mm precipitation) with soils CB1-CB4, were chosen to give a range of soils representative of those widespread throughout the montane eastern South Island.

Three complementary approaches were used : investigation of natural populations (Chapters 1, 2, 3), field transplantation (Chapters 4, 6) and glasshouse experimentation (Chapters 5, 7, 8). To directly compare results, measures of shoot performance, either aerial morphology or DM, were standardized by expressing data as a ratio relative to performance on T4, the main surface at Puffers Stream (Table9.1). Unamended soils were used for the comparison except the legume field transplant experiment where basal nutrients, but no P, were applied.

Table 9.1: Lotus, clover, fescue tussock and matagouri shoot production ranked relative to T4.

Species	Experiment.	Soil T1	T2	T3	T4	T5	CB4
(a) Field							
Lotus	Transplant	0.66	1.47	0.83	1.00	0.90	.
Clover	Transplant	0.43	1.81	0.55	1.00	0.30	.
FNZ	Transplant	1.21	0.99	1.13	1.00	0.90	.
FNZ	Resident	0.84	1.07	0.98	1.00	0.96	.
Matagouri	Resident	12.26	1.00	0.51	1.00	6.01	.
(b) Glasshouse							
Lotus	Pot	0.77			1.00	1.00	0.20
Clover	Pot	0.58			1.00	0.57	0.16
FNZ	Pot	0.56	1.05	0.90	1.00	0.67	0.60
MEAN		**2.16**	**1.23**	**0.82**	**1.00**	**2.43**	**0.32**
MEAN (-Matagouri)		**0.72**	**1.28**	**0.88**	**1.00**	**0.76**	**0.32**

Although the data in Table 9.1 is categorized by soils, a major ecological factor determining vegetation variability in this study, the table unavoidably incorporates the effects of co-factors such as competition (Chapter 6.3), microclimate (Chapter 1.3), pedological variability within a surface (Chapter 1.5) and experimental perturbation (Chapter 7). Though the comparison has been restricted to treatments without applied phosphorus, basal fertilizers could not be separated as a factor from the legume field trial results. Thus Table 9.1 only provides a relative index to assess the effect of natural soil fertility.

Despite such limitations, three conclusions are obvious:

(a) Species differ in response to soil
(b) Soils differ in fertility
(c) (a) and (b) differ depending on experimental technique.

The differences between species can be ranked from Table 9.1 as : matagouri > fescue > lotus > clover. Species edaphic responses are elaborated in following sections (9.1, 9.2 and 9.3).

Soils T1 and T5 differed from other soils in matagouri production. Likewise, soils T2, T3, T4 and probably T5 can be separated from CB4 by legume and fescue growth. Using mean vegetative production excluding matagouri, and also separating T1 on morphological grounds (Chapter 1.4), as soil water holding capacity rather than fertility probably depressed legume yields through poor establishment (Chapter 6.3), the soils can be tentatively ranked in productivity:

T1 >>> T2 > T4 > T3 >? T5 >>> CB4

where >>> indicates a large difference between soil fertility.

This ranking broadly agrees with the age sequence of terraces, leaching regime and pedological development.

The two anomalies are the lower fertility of the youngest soil T1 in the glasshouse experiments (Chapters 5 and 9) and the slightly lower productivity of T3 relative to T4. Fluvial deposition, and subsequent incorporation, of pre-weathered material in the upper profile of T1 could possibly account for the low production but this explanation is not completely satisfying. The difference between T3 and T4, supposedly developed on the same loess mantle with similar deflation history, is even less clear. Presumably it relates to differences in the sub-stratum, T3 comprising debris flow material deposited in a down cut strath of the fluvioglacial gravels that comprise the regolith of T4.

The differences between field and glasshouse results are at least partially due to enhanced N mineralisation from air-drying and sieving soils (Chapter 7).

9.2 MATAGOURI

Edaphic factors are of fundamental importance in the ecology of matagouri as evidenced by its occurrence on young soils and surfaces throughout the South Island and sand dunes in the North Island (Chapter 2.1). The strong negative correlation between matagouri aerial volume and oxalate-extractable aluminium, organic carbon and phosphorus retention (Table2.8) is consistent with this general distribution pattern, though the absence of a strong positive correlation with phosphorus is surprising. Matagouri density, however, was significantly correlated with subsoil phosphorus (Table 2.7). If matagouri has an obligate requirement for high concentrations and availability of nutrients, particularly readily available phosphate, then the ability to obtain nutrients from unweathered subsoil may be an important strategy in nutrient-poor environments. Unfortunately this hypothesis fails to account for the difference in stature between T3 and T4 where subsoil P levels are similar.

Availability of subsoil moisture may determine matagouri growth in conjunction with nutrient availability. Thus the high production on T5 may be due to impeded subsoil drainage improving moisture availability in summer relative to lower terraces (Chapter 1.4). However this explanation is confounded by the possibility of enhanced nutrient supply,

derived from upthrust volcanogenic rock on this surface (Chapter 1.4), also stimulating growth.

Alternatively, sensitivity of matagouri to aluminium or manganese toxicity (Table2.7) may restrict matagouri to young surfaces rather than a there being a simple relationship with P, or other nutrient, availability. Aluminium or manganese may either directly or indirectly inhibit growth through disruption of N fixation or nutrient uptake. This requires further investigation.

Using the concept of plant strategies advanced by Grime (1974, 1977, 1979), though noting the qualifications of Schultz and Chapin (1987), matagouri may be classified as a 'stress-tolerant ruderal'. This classification is made on the basis of its occupancy of disturbed, fertile sites, rapid growth rate and response to nutrient enhancement (Daly 1969), longevity, deep tap root system and intolerance of infertile habitats.

9.3 FESCUE TUSSOCK

Edaphic factors significantly influenced growth of fescue tussock (Table 9.1). Nitrogen and phosphorus are the single most important elements in mineral nutrition on high country yellow brown earth soils (Chapters 2, 3, 4, 5). Sulphur does not appear to be limiting.

In a natural population, tussock density and size were greater on soils which contained greater amounts of P (Tables 2.4, 2.5). Seasonal uptake patterns in shoots showed consistent differences in nutrient supplying power between soils: shoot N concentrations on T1 were consistently higher than on T3 or T5 while shoot P concentrations were consistently lower on T5 relative to other terraces. Shoot sulphur concentrations were similar on all terraces.

Shoot biomass and mineral composition of clonal transplants were closely related to those of resident tussocks on the same terrace (Figs. 4.5, 4.6). Shoot N concentrations and total uptake in transplanted tussocks were highest on T1 and shoot P concentrations lowest on T5. Tussock DM decreased as exchangeable aluminium levels increased in soils, suggesting aluminium toxicity may depress production.

In the glasshouse, phosphorus was the factor responsible for the largest variation in fescue growth. Without applied P, neither N, K, Mg, Ca or S significantly increased DM production above unamended soil. With P, N application increased DM production 3.0 times compared with a 1.7 times increase when only P was applied. Basal K, Mg, Ca and S fertilizer with applied P increased DM production by 1.6 times. Without applied P, high rates of basal depressed yield to only 0.92 times that of untreated soil. This was most probably due to anionic antagonism, inducing P and probably N deficiencies.

The greater P response on the two most pedologically developed soils (T5 and CB4), relative to other soils (Fig. 5.2) is postulated as being caused by aluminium toxicity. Without

applied P, exchangeable aluminium depressed growth until it may have been removed from solution by forming insoluble Al-P complexes with P application.

There was strong evidence for edaphic differentiation between populations of fescue tussock from high and low rainfall environments. The Puffers Stream (low precipitation) population responded to basal fertilizers and DM production increased as soil P levels increased. The Craigieburn population showed no response to basal fertilizers. Craigieburn tussocks outyielded the Puffers Stream population on the soil they originated from, CB4, but did not appreciably differ in yield from the Puffers Stream plants on T4, the original soil of the Puffers Stream population. DM production by the Craigieburn plants increased with increase in soil chemical factors associated with greater pedogenic development (e.g. oxalate extractable aluminium).

These results suggest fescue tussock is a 'C-R-S strategist' with strong affinities to a 'stress-tolerant competitor' (Grime 1979). Its ability to respond to periodic disturbance, obvious from occurrence in such habitats as braided-river beds, is typical of ruderal species. In common with ruderals and competitors, fescue tussock has the capacity for expanded vegetative growth when conditions are favourable. Its slow growth rate, small stature, unpalatability, and ability to tolerate low-nutrient conditions are characteristic of stress tolerant species.

The intraspecific variation, with respect to ecological strategy is similar to that reported for other grasses e.g. *Poa annua* (Low 1978) and *Agrostis tenuis* (Jowett 1964). Ecologically *Festuca novae-zelandiae* appears analogous to *Festuca ovina* in European grasslands and such species as *Bouteloua gracilis, Stipia viridula* and *Sporobolus heterolepis* in the Russian steppes and North American prairies (Grime 1979).

9.4 CLOVER AND LOTUS

Clover and lotus differed in relative dry matter production on different soils, in both field and glasshouse experiments (Table 9.1). Differences in response were due to soil fabric and fertility.

Soil fabric, determining soil moisture holding capacity, was the major factor responsible for the high transplant mortality on T1 and subsequent low production in the field (Table 6.1). Lotus was more sensitive than clover to summer soil moisture deficit during establishment. The higher bulk density of potted T1 soil probably limited growth relative to other soils by higher impedance for roots and by restricting gas and water flux rates.

The interaction between fertilizers, soils and legumes in both field and glasshouse experiments showed that although plant production was determined by a complex of edaphic factors, phosphorus deficiency was the single greatest limiting factor (Chapters 6.3, 7.3, 8.3).

Eighteen months after field transplantation, clover DM production without applied P, increased as soil P fractions increased whereas lotus production did not (Table 6.9). In a

pot experiment using a wider range of soils growth of both legumes was significantly negatively depressed by exchangeable aluminium (Table 8.5). Aluminium had a more severe effect on growth of clover.

In the field trial, clover DM production was only greater than lotus in the first season after establishment (Table 6.5). Conversely, in the glasshouse, lotus production was greater than clover though greater self-shading in clover may have limited expressing its full nutritional response to P. In both experiments, relative lotus DM production was consistently superior to clover at low rates of applied P. Root production decreased in both species with increasing P application. Clover root production was significantly higher than lotus at low P levels.

The N and P concentrations of lotus shoots were lower than in clover in the field and glasshouse experiments, and root N and P concentrations were lower than clover in the glasshouse experiment. In contrast to clover, lotus shoot P concentration in the field trial continued to increase at rates above 50 kg P ha^{-1} with little increase in shoot DM (luxury consumption). However, in the pot trial both P concentrations and DM of both legumes continued to increase with increasing rates of P. Lotus produced more DM per unit P applied than clover with the greatest efficiency of production occurring at lower P rates compared with clover.

Lotus herbage production was significantly greater than clover with or without basal Ca, Mg, K or S fertilizers. The differences narrowed with the addition of basal fertilizers. Lotus uptake of P without basal was greater than clover.

From these results, the edaphic ecology of 'Huia' white clover is clearly typical of a ruderal-competitive plant (Grime 1979) adapted to high fertility soils. It grows quickly and rapidly accumulates mineral resources when they are abundant. Clover's DM productivity is most P-efficient at high P rates but it also demonstrates high phenotypic plasticity by compensatory increase of its root:shoot ratio when nutrient supply decreases. Clover is intolerant of the high exchangeable aluminium concentrations which often occur in infertile habitats.

In contrast 'Maku' lotus is a 'ruderal-competitive' plant which is tolerant of low fertility conditions, thus tending towards a 'stress-tolerant ruderal' species (Grime 1979). Like clover, it responds rapidly to improvement in nutrient supply by increasing shoot and root production. It is also phenotypically plastic and can rapidly capture mineral resources. However, unlike clover it produces proportionately greater biomass at low P levels and in the field, showed a nutrient sequestering capability typical of plants adapted to infertile sites. It is also more efficient in P uptake at low P levels. Lotus, and its rhizobia, are more tolerant of acid soils and exchangeable aluminium than clover. In short, it is adapted to low-medium fertility environments, with the ability to rapidly respond to any improvement in mineral nutrition.

9.5 CONCLUSION

This study investigated the edaphic ecology of fescue tussock, lotus and white clover and also, less intensively, matagouri.

It has shown that pedological development from young recent soils to mature, highly leached Craigieburn HC YBE soils, is a major ecological factor affecting the growth of these species in a typical intermontane eastern South Island basin. Soil fabric, was important as an ecological factor through determining soil water holding capacity. Soil chemistry, controlling nutrient availabilty, is of far wider importance. Soil infertility, principally through P and N deficiencies, and also S, if considering legume requirements, appears to be the major limiting factor. In addition, soil acidity, probably through Al toxicity, is important.

The edaphic ecology of fescue tussock appears that of a 'competitive-ruderal-stress tolerant' species ; white clover a 'ruderal-competitive' species ; lotus a 'ruderal-competitive' species tending towards a 'stress-tolerant' species and matagouri a 'stress tolerant ruderal'species.

ACKNOWLEDGEMENTS

I would like to thank, Professor K.F. O'Connor, Centre for Resource Management, Lincoln College, for his enthusiasm in initiating this project, for his oversight of the tussock study and particularly for assistance with administration and the general supervision of this study,

Dr P. Jarvis, Department of Plant Science, Lincoln College, for his excellent supervision, guidance of the legume experiments, and helpful criticism of the draft manuscript,

Dr A.S. Campbell, Department of Soil Science, Lincoln College, for help with the soil section, and for his friendship and encouragement,

Mr C.L. Batcheler, Forest Research Institute, for generous assistance with data handling and analysis; to Mrs D. Batcheler for her great hospitality,

Dr U. Benecke, Forest Research Institute, for allowing me time to complete this project,

Dr R. Harrison, Department of Soil Science, Lincoln College, for allowing use of unpublished soil chemical data,

Paul Garven, Agricultural Engineering Institute, Lincoln College, for assistance with the meteorological station,

Graeme Hall, Forest Research Institute, for writing a programme to assist with checking references,

Tom Pearson, Margaret Clark, and Natalie Vickers, of the Forest Research Institute, for help with the figures,

Murray Lang, Forest Research Institute, for assisting with nutrient analyses,

Gareth Grimes, Laurie Bennet and Mary Sullivan for help in the glasshouse and the laboratory,

My mother for her help in the field and for reading meteorological charts,

Marie Bussieres, for help and encouragement during the early stages of this study,

Janet and Bruce Warburton, for a first class job typing the text and tables,

Steve Hough, Forest Research Institute, for his outstanding help in preparing the thesis for binding,

Dianne, my wife, for her tremendous love, support and assistance in the long period of writing, the many friends, particularly Lawrence Heath, Dave & Virginia Askin, for help and encouragement.

the Miss E.L. Hellaby Indigenous Grasslands Research Trust and the University Grants Committee for providing the finance which made this study possible,

and Wolfgang Amadaeus Mozart : Eine Kleine Nachtmusik was the theme of this thesis, in more ways than one!

Sola deo gloria

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APPENDICES

APPENDIX 1.1 : ACTINOGRAPH CALIBRATION

The actinograph (Serial No. 115693) was calibrated against the Lincoln College Sub Standard Pyranometer Eppley PSP 181242 . The Lincoln pyranometer was itself previously calibrated against the N.Z.Meterorological Service National Reference Eppley Angstrom Electrical Compensation pyrheliometer in February 1981 and subsequently only used for calibration . Its Calibration constant was determined to be 9.8 mV . kW-1 . m-2. (W.R.R.) .

The actinograph and reference pyranometer were mounted 50cm apart on the Roof of the Hilgendorf Wing , Lincoln College , on the 30th June , 1982 . Bulb levels were arbitralily aligned due West and both instruments were leveled . Simultaneous measurement of the Eppley output voltage , using a Hewlet - Packard multivoltmeter and the actinograph chart position were made at approximately half hour intervals during the 7th July under clear sky conditions .

The voltage output from the Eppley was linear in relation to actinograph chart recording , with a distinct hysteresis depending on whether the instrument was heating or cooling (Fig. 1) .

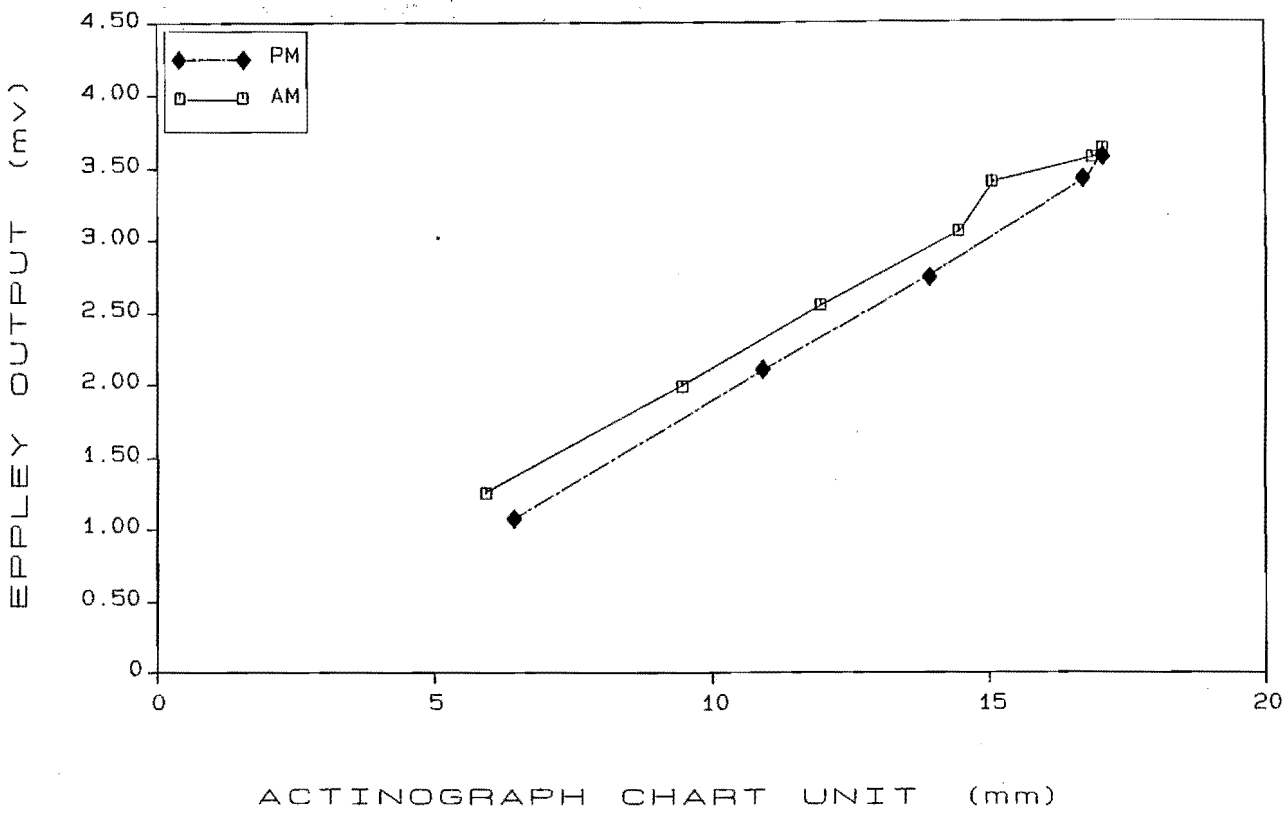

Figure 1 : Eppley voltage output vs Actinograph chart unit.

The actual relationships , excluding the zenith reading at 12.30 am , were :-

AM Eppley (mv) = - 0.019 + 0.215 Act. Unit (mm) R = 0.993

PM Eppley (mv) = - 0.372 + 0.225 Act. Unit (mm) R = 1.000

The small improvement in accuracy by attempting to correct for hysteresis was not attempted in view of the labour involved and the inherent accuracy of the instrument.

Therefore the mean regression through all points , irrespective of hysteresis , was derived . The relationship

after conversion using the Eppley calibration constant , was:-

Wm-2 = -0.0197 + 0.0227 Act. Unit (mm) R = 0.982

This equation was used for the conversion of all Chart data.

APPENDIX 1.2 : ANEMOMETER CALIBRATION

Two Munro totalising anemometers were calibrated in the Lincoln College Agricultural Engineering and D.S.I.R. Civil and Industrial Development Division Wind Tunnels before field use.

Wind run at constant airflow was recorded on each anemometer in the College tunnel at 1 to 2 minute intervals. Air velocity was measured during the duration of the experiment as 4.2 m/sec (S.E. 0.02 , n=18) with an " Alnor " 8500 thermoanemometer, calibrated a week previously to within 1% absolute error (D.S.I.R. unpublished Test Report, 28th September, 1982).

Both instruments gave identical results (Fig. 1) . but overestimated the true wind run.

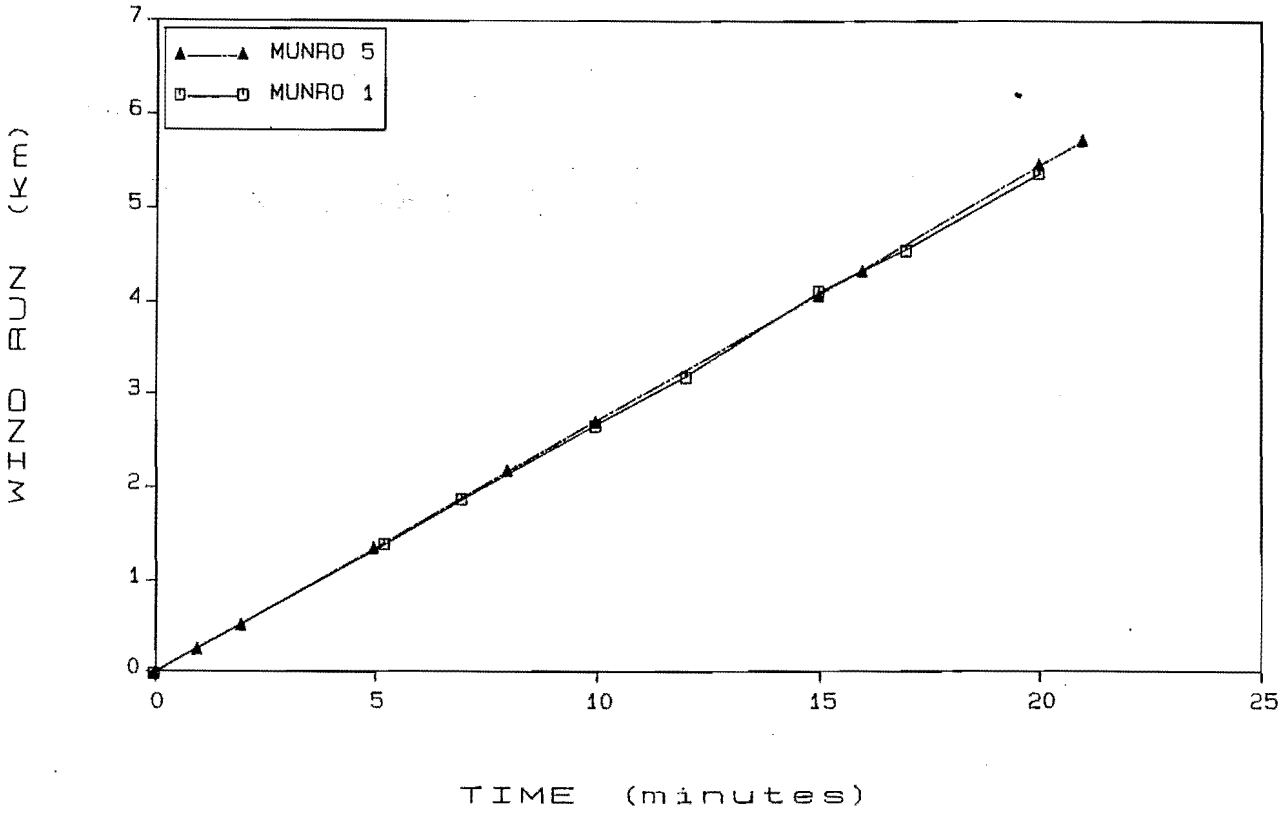

Figure 1 : Windrun recorded by two Munro anemometers at constant wind speed.

Correction factors were derived as follows :-

C. Factor = $\frac{\text{Mean instantaneous windspeed x time}}{\text{Instrumental recorded windspeed}}$

= Monro 1 Serial No 2977 (Terrace One)	0.939
= Monro 5 Serial No 2932 (Terrace Five)	0.923

These factors were used to correct all subsequent field data.

Wind run recorded at variable airflows in the D.S.I.R. tunnel showed one anemometer to give slightly higher readings at airflows between 10 to 30 m/sec (Fig. 2).

As most windspeeds in the field were less then this (Section 1.3.3.2) the total error introduced is likely to be very small . No attempt to compensate for this bias was made . The instrument placed on terrace one would thus slightly over-record relative to terrace five .

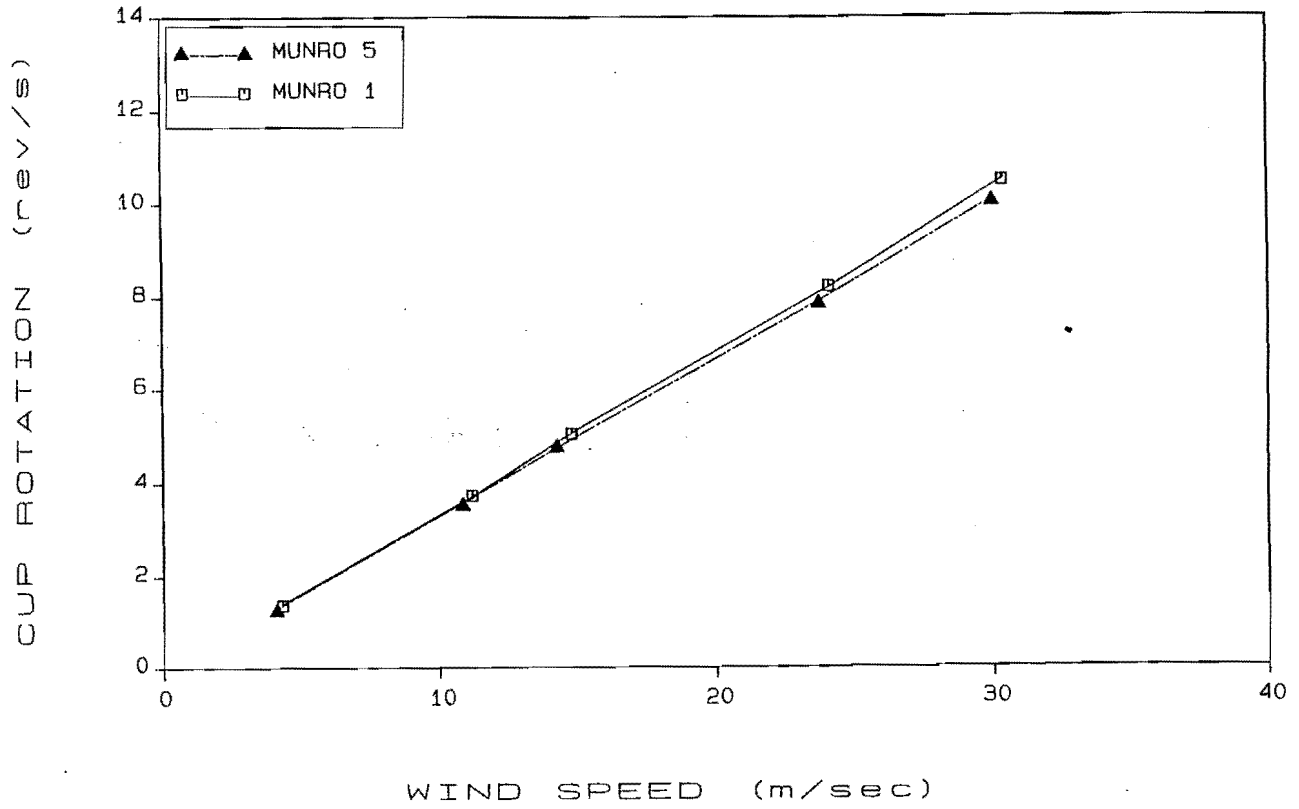

Figure 2 : Windrun recorded by two Munro anemometers at variable wind speed.

APPENDIX 1.3: FLORA RECORDED AT SLOVENS STREAM

BRYOPHYTA : MUSCI

BRYALES

Polytrichaceae

Polytrichum juniperinum

Grimmiaceae

Racomitrium lanuginosum

Dicranaceae

Campylopus clavatus

PTERIDOPHYTA

FILICOPSIDA

Ophioglossacea

Ophioglossum coriacea

SPERMATOPHYTA

ANGIOSPERMAE

DICOTYLEDONAE

Cruciferae

Cardamine debilis

Violaceae

Hymenanthera alpina
Viola cunninghamii

Caryophyllaceae

Cerastium fontanum *
Colobanthus buchananii
Dianthus armeria *
Scleranthus uniflorus

Polygonaceae

Muehlenbeckia axillaris
Rumex acetosella *

Geraniaceae

Geranium sessiliflorum

Linaceae

Linum catharticum

Haloragaceae

Gonocarpus aggregatus

Onagraceae

Epilobium alsinoides

Thymelaeaceae

Pimelea oreophila

Myrtaceae

Leptospermum scoparium

Rosaceae

Acaena caesiiglauca
Acaena inermis
Rosa rubiginosa *

Papilionaceae

Carmichaelia monroi
Carmichaelia robusta
Carmichaelia uniflora
Lotus pedunculatus * *(sown this study)*
Trifolium arvense *
Trifolium dubium *
Trifolium pratense *
Trifolium repens *
Ulex europaeus *

Rhamnaceae

Discaria toumatou

Umbelliferae

Aciphylla aurea
Anisotome aromatica
Anisotome filifolia
Oreomyrrhis colensoi

Epacridaceae

Cyathodes colensoi
Cyathodes fraseri (= Leucopogon fraseri)

Rubiaceae

Coprosma atropurpurea
Coprosma petriei
Coprosma propinqua
Coprosma rugosa

Compositae

Cassinia fulvida
Brachycome sinclairii
Celmisia gracilenta
Celmisia spectabilis
Craspedia uniflora
Crepis capillaris
Gnaphalium audax
Helichrysum bellidioides
Helichrysum filicaule
Hieracium lachenalii
Hypochaeris radicata
Microseris scapigera
Pilosella officinarum (syn. *Hieracium pilosella*)
Raoulia subsericea
Brachyglottis bellidioides (= Senecio bellidioides)

Gentianaceae

Gentiana grisbachii
Gentiana corymbifera

Plantaginaceae

Plantago lanceolata *
Plantago spathulata

Campanulaceae

Wahlenbergia albomarginata

Boraginaceae

Myosotis uniflora

MONOCOTYLEDONAE

Juncaceae

Luzula rufa var. rufa

Cyperaceae

Carex breviculmis

Graminae

Agrostis tenuis
Aira caryophyllea *
Anthoxanthum odoratum *
Chionochloa macra x flavescens
Chionochloa rigida
Chionochloa rubra
Deyeuxia avenoides
Dichelachne crinita
Festuca novae-zelandiae
Holcus lanatus *
Lachnagrostis filiformis
Poa cita (= Poa caespitosa)
Poa colensoi
Poa pratensis *
Rytdiosperma gracile

Orchidaceae

Microtis oligantha
Prasophyllum colensoi

Nomenclature

** indicates an adventive species.*

Arrangement and nomenclature is after Sainsbury (1955), Allan (1961), Moore and Edgar (1970), and Clapham,Tutin and Moore (1987) . Epilobium follows Raven and Raven (1976) ; Gonocarpus, Orchard (1975) ; Gnaphalium, Drury (1972) ; Graminae, Cheeseman 1925, Zotov (1943, 1963, 1970) Edgar, 1986; Pimelia, Burrows (1962) .

APPENDIX 2.1 : FESCUE TUSSOCK ASSOCIATIONS IN NEW ZEALAND (after BLASCHKE et al. 1981)

VEGETATION CLASS			VEGETATION CATEGORY	AREA (ha) N.I.	S.I.	% AREA N.I.	S.I.
(A) GRASSLAND							
G3	Tussock associations with short tussock	g7	Short tussock	1 900	133 100	<.1	0.9
		g8	Short & snow tussock	600	724 700	<.1	4.8
		g9	Short & red tussock	3 300	18 700	<.1	0.1
		g10	Mixed short, snow & red tussock	—	7 200		<.1
				58 00	883 700	0.1	5.9
G5	Mixed short tussock & pasture associations	g15	Short tussock & improved pasture	400	29 900		0.2
		g16	Short tussock & unimproved pasture	3 100	315 500	<.1	2.1
		g17	Short & snow tussock & pasture	—	37 600		0.3
		g18	Short tussock & mixed un/improved pasture	—	28 100		0.2
				3 500	411 100	<.1	2.7
(B) GRASSLAND - SCRUB							
GS1	Grassland & mixed indigenous scrub	gs2	Short tussock & mixed indigenous scrub	3 000	75 000	<.1	0.5
		gs3	Short tussock, pasture mixed indigenous scrub	300	74 200	<.1	0.5
				3 300	79 200	<.1	1.0
GS2	Grassland, fern & *Leptospermum* scrub	gs5	Short tussock & *Leptospermum*	37 300	87 600	0.3	0.9
		gs6	Short tussock, pasture & *Leptospermum*	5 400	49 500	<.1	0.3
		gs8	Short tussock & fern	300	76 300	<.1	0.5
		gs10	Pasture /Short tussock *Leptospermum* / fern	133 500	116 200	1.2	0.8
		gs11	Short tussock, fern & *Leptospermum*	300	60 800	<.1	0.4
				176 800	390 400	1.5	2.6
GS4	Grassland & scrub containing gorse	gs16	Short tussock, pasture & gorse	—	25 500		0.2
		gs17	Short tussock / pasture gorse & *Leptospermum*	—	5 600		<.1
		gs18	Short tussock, gorse & mixed indigenous scrub	—	9 500		0.1
		gs19	Short tussock / pasture gorse & *Leptospermum*	—	19 000		0.1
		gs21	Pasture / short tussock gorse & fern	11 700	71 400	0.1	0.5
		gs22	Short tussock, gorse & fern	—	7 200		<.1
		gs25	Short tussock, gorse & other scrub	—	3 600		<.1
				11 700	141 800	0.1	0.9
GS7	Grassland, sweet briar & matagouri	gs30	Short tussock, pasture & sweet briar	—	69 800		0.5
		gs32	Short, snow tussock & matagouri	—	174 300		1.2
		gs33	Short tussock, matagouri unimproved pasture	—	350 000		2.3
		gs35	Short tussock, matagouri sweet briar	—	62 800		0.5
		gs36	Short tussock, pasture sweet briar & matagouri	—	73 000		0.5
		gs37	Pasture/ Short tussock sweet briar & other scrub	—	3 100		<.1
		gs38	Short tussock, sweet briar & other scrub	—	10 100		0.1
		gs39	Short tussock, matagouri, unimp. pasture other scrub	—	38 200		0.2
		gs40	Short/ snow/ red tussock, matagouri & other scrub	—	50 600		0.3
				—	831 900		5.5

GS11	Grassland, scrub & semi- arid herbs	gs46	Short tussock, matagouri/ sweet briar,semi- arid herbs	_	11 600	0.1
		gs49	Short tussock, pasture scrub & semi- arid herbs	_	48 400	0.3
				_	50 000	0.4

APPENDIX 2.2 : SOIL CHEMICAL PARAMETERS

CODE	PARAMETER	REFERENCE
pH	pH in water (1:2.5 w:v)	Blakemore *et al.* 1981
pHCl	pH in 0.01M CaCl (1:2.5 w:v)	"
Fe_o	Oxalate extractable iron	"
Al_o	Oxalate extractable aluminium	"
Si_o	Oxalate extractable silicon	"
Fe_p	Pyrophosphate extractable iron	"
Al_p	Pyrophosphate extractable aluminium	"
Si_p	Pyrophosphate extractable silicon	"
Fe_e	EDTA extractable iron	Farmer *et al.* 1981
Al_e	EDTA extractable aluminium	"
NaF	pH in NaF (5min)	Blakemore *et al.* 1981
Pret	Phosphorus retention	"
C	Carbon %	"
N	Nitrogen %	"
LOI	Loss on Ignition at 1000 °C	"
Ptot	Total Phosphorus	"
Porg	Total Organic Phosphorus	"
Pap	Total Inorganic Phosphorus	"
Pxrf	P_2O_5 % total weight	Harrison & Swift 1984
CEC	Cation Exchange Capacity pH 7.0	Blakemore *et al.* 1981
ECEC	Effective Cation Exchange Capacity	"
TEB	Total Exchangable Base Cations	"
BS_C	% Base Saturation CEC	"
BS_E	% Base Saturation ECEC	"
Ca	Exchangable Calcium	"
Mg	Exchangable Magnesium	"
K	Exchangable Potassium	"
Na	Exchangable Sodium	"
Al	Exchangable Aluminium	"
H	Exchangable Hydrogen	"

The actual values of the parameters are listed for soils T1-T5 by 10 cm horizons in Harrison & Swift (1985).

APPENDIX 2.3 : CHEMICAL ANALYSES

(a) Nitrogen

Ground samples and a standard composite tussock sample were dried at 75°C for 2 hours and cooled in a dessicator for 1/2 hour and 0.100 to 0.200 g sample was weighed into a micro-kjeldahl digestion flask. Samples were duplicated unless insufficient material was present. Reagent blanks and the standard sample were included with each digestion run.

1 g catalyst (100g K_2SO_4 : 10g $CuSO_4$: lg Se) was added by scoop to the flask and 3.0 ml concentrated sulphuric acid A.R. added by pippette. Flasks were heated in a sand bath to ca. 180 °C and boiled until bright green. Digestates plus 15 ml sodium hydroxide solution were steam distilled into boric acid plus indicator solution until the indicator changed colour and approximately 30 ml distilled solution had been collected. This was back-titrated with 0.05 M sulphuric acid ± 0.01 ml (Blakemore *et al.* 1981).

Reagents were as follows:

Catalyst: 100g K_2SO_4: 10g $CuSO_4.5H_2O$:1g Se

Sulphuric acid for titration: (0.05 MH_2SO_4): 25 ml 0.5 M made to 500 ml with distilled water.

Sodium hydroxide: 1 kg ± 10 g NaOH added to 2l distilled water.

Boric acid 1: 40 g boric acid added to 2l distilled water to make 2% solution.

0.032 g bromocresol green and 0.008 methyl red was dissolved in 200 ml 96% ethanol. 5 ml of indicator solution was added per litre of boric acid.

(b) Phosphorus and Sulphur

Fifteen ground samples and a standard composite tussock sample were dried at 70°c for 2 to 4 hours and cooled in a dessicator. 0.250 ± 0.002 g sample or less if insufficient, was weighed into a digest tube and 3 ml of a 2 : 3 mixture of Perchloric Acid A.R. : concentrated Nitric Acid A.R. was added to each digest tube and left to stand overnight.

Fifteen samples and the standard sample were duplicated in two 16 tube digestion blocks; heated to approximately 180 °C over 1 hour then raised to 225 °C for thirty

minutes. Digests were cooled, 10 ml distilled water added and left to stand. Each digest was quantitatively transferred to a 50.0 ml volumetric flask and made to volume. Solutions were stored in polythene bottles prior to macro-element analysis.

Phosphorus

Digests were diluted using a Hati variable auto diluter, 15.0 ml distilled water being added to 0.50 ml digest solution and stored in a glass vial immediately prior to analysis. Solution P concentration was determined colourimetrically using the molybdenum blue reaction on a Technicon Auto-analyser. (Technicon, pers. comm.).

Sulphur

Sulphate was determined turbidimetrically (Garrido 1964) on a Chem. Lab. CS40 autoanalyser with EDTA and Brij 35 wash solutions between samples.

1.25 ml buffer solution (75 ml glacial acetic acid; 30 ml concentrated Hydrocloric acid A.R.; 30 ml Orthophosphoric acid and 0.1087g potassium sulphate A.R. made up to 1000 ml) was added to 5.0 ml digest solution using the automatic diluter and stored in a glass vial immediately prior to S analysis. The precipitant solution (8.0 g Barium Chloride and 10 ml Tween 80 added to 200 ml distilled water) was made up immediately before each analysis run. The wash solutions were 25 g EDTA disodium salt and 25 g sodium hydroxide made up to 100 ml with distilled water and Brij 35 (2% weight: volume). The carrier solution consisted of 50 ml concentrated hydrochloric acid made up to 1000 ml with distilled water.

APPENDIX 2.4 : CORRELATION COEFFICIENTS OF FESCUE TUSSOCK DENSITY AND SOIL CHEMICAL PARAMETERS BETWEEN 0 - 100 CM DEPTH ON T1-T4

Correlation Coefficient (r) ;
Significance probability ;
sample number (n = 5 unless otherwise shown)

DEPTH	SOIL PARAMETER #					
(cm)	PH	PHCL	P_XRF	P_TOT	P_AP	P_ORG
0-10	0.42240	-0.68404	0.86503	0.90683	0.81539	0.91536
	0.4786	0.2028	0.0583	0.0337	0.0925	0.0292
20-30	-0.03777	-0.05615	0.89057	0.89342	0.64441	0.94198
	0.9519	0.9285	0.0427	0.0411	0.2405	0.0166
30-40	-0.19360	-0.16145	0.88252	0.87413	0.32568	0.93808
	0.7551	0.7953	0.0475	0.0526	0.5928	0.0183
40-50	-0.60213	-0.41526	0.84623	0.85810	0.39608	0.91934
	0.2826	0.4869	0.0707	0.0628	0.5092	0.0272
50-60	-0.52208	-0.76201	0.87179	0.84636	0.42865	0.97590
	0.3668	0.1343	0.0540	0.0706	0.4714	0.0045
60-70	-0.40505	-0.62742	0.75240	0.82420	0.53934	0.84691
	0.4987	0.2572	0.1423	0.0861	0.3482	0.0702
70-80	-0.34140	-0.50966	0.69450	0.72554	0.73724	0.15149
	0.5739	0.3804	0.1931	0.1653	0.1552	0.8079
80-90	-0.49256	-0.45862	0.81013	0.83948	0.83633	0.42989
	0.3992	0.4372	0.0964	0.0753	0.0775	0.4700
90-100	-0.44508	-0.55868	-0.33425	0.68233	0.44937	0.87268
	0.4526	0.3276	0.7830	0.3177	0.5506	0.1273
	5	5	5	4	4	4
100-110	-0.6274	-0.54345	0.53183	.	.	.
	0.2572	0.3438	0.3563			
	5	5	5	1	1	1

Parameter codes are shown in Appendix 2.2

Appendix 2.4 (continued)

DEPTH	SOIL PARAMETER #				
(cm)	P_RET	NaF	N	C	LOI
0-10	0.59059 0.2944	0.46323 0.4320	0.67919 0.2073	0.61586 0.2687	0.61396 0.2706
20-30	0.51413 0.3755	0.45314 0.4435	0.84260 0.0732	0.88378 0.0467	0.65770 0.2277
30-40	0.48709 0.4053	0.47318 0.4208	0.84583 0.0710	0.87763 0.0504	0.85336 0.0659
40-50	0.44337 0.4546	0.39862 0.5062	0.80187 0.1027	0.74228 0.1508	0.65947 0.2260
50-60	0.64872 0.2363 5	0.40053 0.5040 5	0.92695 0.0730 4	0.90565 0.0944 4	0.90364 0.0354 5
60-70	0.96093 0.0391 4	0.48477 0.4079 5	1.00000 0.0000 2	0.99387 0.0705 3	0.56999 0.3157 5
70-80	0.95598 0.0440 4	0.39212 0.5138 5	. 1	1.00000 0.0000 2	0.53684 0.3509 5
80-90	0.89006 0.1099 4	0.62437 0.2602 5	. 0	. 0	0.54828 0.3387 5
90-100	1.00000 0.0000 2	0.54277 0.3445 5	. 0	. 0	0.75895 0.4514 3
100-110	. 0	0.53116 0.3570 5	. 0	. 0	. 0

Parameter codes are shown in Appendix 2.2

Appendix 2.4 (continued)

DEPTH	SOIL PARAMETER #					
(cm)	SI_O	FE_O	AL_O	AL_P	FE_P	AL_
0-10	-0.33324	0.67398	0.59635	0.74738	0.84829	0.6758
	0.5837	0.2122	0.2885	0.1465	0.0693	0.210
20-30	-0.03439	0.55868	0.51044	0.67730	0.57975	0.5906
	0.9562	0.3276	0.3795	0.2091	0.3056	0.294
30-40	0.01036	0.45334	0.58611	0.50533	0.56026	0.8513
	0.9868	0.4432	0.2990	0.3851	0.3260	0.067
40-50	0.02062	0.29310	0.78564	0.59355	0.83441	0.6142
	0.9738	0.6322	0.1152	0.2913	0.0788	0.270
50-60	0.11848	0.50881	0.86946	0.83663	0.95776	0.9115
	0.8495	0.3813	0.0555	0.1634	0.0422	0.088
	5	5	5	4	4	4
60-70	0.63713	0.84391	0.82922	1.00000	1.00000	1.0000
	0.2476	0.0723	0.0825	0.0000	0.0000	0.0000
	5	5	5	2	2	
70-80	0.56909	0.73349	0.20541	.	.	.
	0.3167	0.1584	0.7403			
	5	5	5	1	1	
80-90	0.88228	0.91295	0.39193	.	.	.
	0.0476	0.0304	0.5141			
	5	5	5	0	0	
90-100	0.78954	0.80886	-0.11732	.	.	.
	0.1122	0.0974	0.8510			
	5	5	5	0	0	
100-110.	.	.	.	.	.	.
	0	0	0	0	0	

Parameter codes are shown in Appendix 2.2

Appendix 2.4 (continued)

DEPTH	SOIL PARAMETER #					
(cm)	FE_E	TEB	AL_EX	CEC	ECEC	BS_C
0-10	-0.18705	-0.24004	0.37329	0.57568	-0.15316	-0.48620
	0.7632	0.6973	0.5360	0.3098	0.8058	0.4063
20-30	-0.17308	-0.02181	-0.12563	0.78590	-0.20784	0.04847
	0.7807	0.9722	0.8405	0.1150	0.7373	0.9383
30-40	0.65334	-0.13163	-0.10790	0.90405	-0.31782	-0.26790
	0.2318	0.8329	0.8629	0.0352	0.6023	0.6630
40-50	0.55616	-0.40250	0.35600	0.87941	-0.28626	-0.43810
	0.3303	0.5017	0.5565	0.0494	0.6406	0.4606
50-60	0.60770	0.16832	0.95272	0.98533	0.70023	-0.22218
	0.3923	0.8317	0.0473	0.0147	0.2998	0.7778
	4	4	4	4	4	4
60-70	1.00000	1.00000	1.00000	1.00000	1.00000	1.00000
	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000
	2	2	2	2	2	2
70-80	.	.	.	.	.	.
	1	1	1	1	1	1

Parameter codes are shown in Appendix 2.2

Appendix 2.4 (continued)

DEPTH	SOIL PARAMETER #					
(cm)	BS_E	CA	MG	K	NA	
0-10	-0.25644	-0.37418	0.26845	0.33903	-0.27953	-0.0584
	0.6771	0.5349	0.6623	0.5768	0.6488	0.925
20-30	0.00682	-0.03275	-0.02711	0.11755	-0.13067	0.1123
	0.9913	0.9583	0.9655	0.8507	0.8341	0.857
30-40	-0.03147	-0.09299	-0.29169	-0.19925	-0.23005	-0.2460
	0.9599	0.8818	0.6339	0.7480	0.7097	0.689
40-50	-0.42064	-0.36030	-0.47752	-0.39630	0.30112	0.6752
	0.4807	0.5514	0.4160	0.5089	0.6225	0.211
50-60	-0.404720	0.16891	0.01831	0.79685	0.12223	0.1040
	0.5953	0.8311	0.9817	0.2032	0.8778	0.895
	4	4	4	4	4	
60-70	1.000000	1.00000	1.00000	1.00000	1.00000	1.0000
	0.0000	0.0000	0.0000	0.0000	0.0000	0.000
	2	2	2	2	2	
70-80	.	.	.	.	.	.
	1	1	1	1	1	

Parameter codes are shown in Appendix 2.2

APPENDIX 2.5 : CORRELATION COEFFICIENTS OF FESCUE TUSSOCK BASAL AREA AND SOIL CHEMICAL PARAMETERS BETWEEN 0 - 100 CM DEPTH ON T1-T4

Correlation Coefficient (r) ;
Significance probability ;
sample number (n = 5 unless otherwise shown)

DEPTH	SOIL PARAMETER #					
(cm)	PH	PHCL	P_XRF	P_TOT	P_AP	P_OR
0-10	-0.71040	-0.65858	0.75470	0.87185	0.94945	0.8253
	0.1787	0.2268	0.1404	0.0540	0.0135	0.085
20-30	-0.43312	-0.40679	0.75279	0.77775	0.70640	0.7791
	0.4663	0.4967	0.1419	0.1215	0.1823	0.120
30-40	-0.57685	-0.44634	0.68269	0.70090	0.36142	0.7021
	0.3086	0.4512	0.2040	0.1873	0.5500	0.186
40-50	-0.86493	-0.74028	0.48223	0.48673	0.11074	0.5767
	0.0584	0.1525	0.4107	0.4057	0.8593	0.308
50-60	-0.80340	-0.88280	0.43839	0.40608	-0.05470	0.7003
	0.1015	0.0473	0.4603	0.4975	0.9304	0.187
60-70	-0.56847	-0.84007	0.27734	0.35195	0.12136	0.4576
	0.3173	0.0749	0.6515	0.5613	0.8459	0.438
70-80	-0.62665	-0.81499	0.17583	0.24070	0.40301	-0.2524
	0.2580	0.0928	0.7773	0.6965	0.5011	0.682
80-90	-0.68528	-0.69072	0.32474	0.42434	0.62694	-0.0884
	0.2016	0.1966	0.5939	0.4764	0.2577	0.887
90-100	-0.67933	-0.70718	-0.97705	0.54583	0.49493	0.5021
	0.2072	0.1816	0.1367	0.4542	0.5051	0.497
	5	5	3	4	4	
100-110	-0.84007	-0.70945	0.044730	.	.	.
	0.0749	0.1796	0.9431			
	5	5	5	1	1	

Parameter codes are shown in Appendix 2.2

Appendix 2.5 (continued)

DEPTH	SOIL PARAMETER #				
(cm)	P_RET	NaF	N	C	LOI
0-10	0.64138	0.27285	0.78045	0.91223	0.76119
	0.2435	0.6570	0.1193	0.0308	0.1350
20-30	0.71077	0.35609	0.68731	0.83659	0.84546
	0.1784	0.5564	0.1998	0.0773	0.0712
30-40	0.74470	0.65164	0.71294	0.79604	0.93199
	0.1488	0.2335	0.1765	0.1071	0.0211
40-50	0.67633	0.55283	0.64973	0.64818	0.78364
	0.2100	0.3338	0.2353	0.2368	0.1168
50-60	0.85392	0.71978	0.93207	0.81238	0.87730
	0.0655	0.1704	0.0679	0.1876	0.0506
	5	5	4	4	5
60-70	0.72456	0.79556	1.00000	0.61801	0.14142
	0.2754	0.1075	1.0000	0.5759	0.8205
	4	5	2	3	5
70-80	0.50817	0.69497	.	1.00000	-0.05534
	0.4918	0.1927		0.0000	0.9296
	4	5	1	2	5
80-90	0.43640	0.79884	.	.	0.04018
	0.5636	0.1050			0.9488
	4	5	0	0	5
90-100	1.00000	0.81011	.	.	-0.15302
	1.0000	0.0965			0.9022
	2	5	0	0	3
100-110	.	0.76521	.	.	.
		0.1317			
	0	5	0	0	0

Parameter codes are shown in Appendix 2.2

Appendix 2.5 (continued)

DEPTH	SOIL PARAMETER #					
(cm)	SI_O	FE_O	AL_O	AL_P	FE_P	AL_E
0-10	-0.62884	0.67937	0.72850	0.71825	0.78869	0.8106
	0.2558	0.2071	0.1627	0.1717	0.1128	0.096
20-30	0.00706	0.63182	0.72861	0.72733	0.76696	0.8143
	0.9910	0.2528	0.1626	0.1637	0.1302	0.093
30-40	0.19633	0.63619	0.78554	0.67520	0.75710	0.9613
	0.7516	0.2485	0.1153	0.2110	0.1384	0.009
40-50	0.10573	0.38909	0.99777	0.70805	0.92259	0.7284
	0.8656	0.5174	0.0001	0.1808	0.0256	0.162
50-60	0.39765	0.71544	0.68797	0.82529	0.79211	0.9447
	0.5074	0.1742	0.1991	0.1747	0.2079	0.055
	5	5	5	4	4	4
60-70	0.78235	0.90536	0.41059	1.00000	1.00000	1.0000
	0.1178	0.0345	0.4923	1.0000	1.0000	1.0000
	5	5	5	2	2	
70-80	0.71985	0.84395	-0.27376	.	.	.
	0.1703	0.0722	0.6558			
	5	5	5	1	1	
80-90	0.73984	0.72491	-0.09708	.	.	.
	0.1529	0.1659	0.8766			
	5	5	5	0	0	
90-100	0.79942	0.81672	-0.48880	.	.	.
	0.1045	0.0916	0.4034			
	5	5	5	0	0	

Parameter codes are shown in Appendix 2.2

Appendix 2.5 (continued)

DEPTH	SOIL PARAMETER #					
(cm)	FE_E	TEB	AL_EX	CEC	ECEC	BS_C
0-10	0.27073	-0.02246	0.23709	0.94349	0.12404	-0.51681
	0.6596	0.9714	0.7010	0.0160	0.8425	0.3726
20-30	0.32238	-0.42198	0.20202	0.89766	-0.29879	-0.39268
	0.5968	0.4791	0.7445	0.0387	0.6253	0.5132
30-40	0.64636	-0.55202	0.14576	0.80121	-0.57084	-0.64534
	0.2386	0.3347	0.8151	0.1032	0.3149	0.2396
40-50	0.51813	-0.66006	0.58959	0.91900	-0.47309	-0.70209
	0.3711	0.2254	0.2954	0.0273	0.4209	0.1862
50-60	0.96279	0.76045	0.70641	0.67791	0.89704	0.45514
	0.0372	0.2396	0.2936	0.3221	0.1030	0.5449
	4	4	4	4	4	4
60-70	1.00000	1.00000	1.00000	1.00000	1.00000	1.00000
	1.0000	1.0000	1.0000	1.0000	1.0000	1.0000
	2	2	2	2	2	2
70-80	.	.	.	.	.	.
	1	1	1	1	1	1

Parameter codes are shown in Appendix 2.2

Appendix 2.5 (continued)

DEPTH	SOIL PARAMETER #					
(cm)	BS_E	CA	MG	K	NA	H
0-10	-0.14368	-0.25125	0.59740	0.78144	-0.36781	0.46669
	0.8177	0.6835	0.2874	0.1186	0.5425	0.4281
20-30	-0.38050	-0.40381	-0.44114	-0.34735	-0.43019	0.52264
	0.5275	0.5002	0.4571	0.5668	0.4697	0.3662
30-40	-0.45559	-0.51939	-0.67112	-0.49926	-0.49508	-0.09362
	0.4407	0.3698	0.2149	0.3918	0.3964	0.8810
40-50	-0.67856	-0.67785	-0.75244	-0.69120	-0.21521	0.90859
	0.2079	0.2086	0.1422	0.1962	0.7281	0.0327
50-60	0.30775	0.78008	0.44048	0.39919	-0.01837	0.34832
	0.6922	0.2199	0.5595	0.6008	0.9816	0.6517
	4	4	4	4	4	4
60-70	1.00000	1.00000	1.00000	1.00000	1.00000	1.00000
	1.0000	1.0000	1.0000	1.0000	1.0000	1.0000
	2	2	2	2	2	2
70-80	.	.	.	.	.	.
	1	1	1	1	1	1

Parameter codes are shown in Appendix 2.2

APPENDIX 2.6 : CORRELATION COEFFICIENTS OF MATAGOURI DENSITY AND SOIL CHEMICAL PARAMETERS BETWEEN 0 - 100 CM DEPTH ON T1-T4

Correlation Coefficient (r) ;
Significance probability ;
sample number (n=5 unless otherwise shown)

DEPTH	SOIL PARAMETER #					
(cm)	PH	PHCL	P_XRF	P_TOT	P_AP	P_OR
0-10	-0.08027	-0.44445	0.48433	0.48239	0.26829	0.5403
	0.8979	0.4533	0.4084	0.4105	0.6625	0.347
20-30	0.19422	0.28002	0.61140	0.60014	0.24191	0.6888
	0.7543	0.6482	0.2732	0.2846	0.6950	0.198
30-40	0.08059	0.30433	0.69698	0.66745	0.12047	0.7910
	0.8975	0.6186	0.1909	0.2184	0.8470	0.111
40-50	-0.25668	0.17391	0.83379	0.80538	0.41562	0.8549
	0.6768	0.7797	0.0793	0.1000	0.4865	0.064
50-60	-0.17109	-0.36210	0.90628	0.89856	0.85418	0.7317
	0.7832	0.5492	0.0340	0.0382	0.0654	0.159
60-70	-0.28917	-0.24866	0.90547	0.90641	0.89381	0.6038
	0.6370	0.6867	0.0344	0.0339	0.0409	0.280
70-80	-0.17192	-0.07302	0.94924	0.94693	0.93838	0.28874
	0.7822	0.9071	0.0136	0.0146	0.0182	0.637
80-90	-0.27755	-0.10115	0.86790	0.81899	0.81687	0.4424
	0.6512	0.8714	0.0565	0.0899	0.0914	0.455
90-100	-0.26235	-0.25476	0.48475	0.77465	0.56455	0.5696
	0.6698	0.6792	0.6778	0.2253	0.4354	0.430
	5	5	3	4	4	
100-110	-0.2487	-0.23404	0.93029	.	.	.
	0.6867	0.7048	0.0219			
	5	5	5	1	1	

Parameter codes are shown in Appendix 2.2

Appendix 2.6 (continued)

DEPTH	SOIL PARAMETER #				
(cm)	P_RET	NaF	N	C	LOI
0-10	0.59069	0.77174	0.37388	0.17032	0.29180
	0.2943	0.1263	0.5353	0.7842	0.6338
20-30	0.39360	0.63260	0.77263	0.66626	0.41131
	0.5121	0.2521	0.1256	0.2195	0.4915
30-40	0.29127	0.42004	0.72108	0.67339	0.45288
	0.6345	0.4814	0.1692	0.2127	0.4437
40-50	0.31913	0.43328	0.71090	0.72860	0.40355
	0.6007	0.4661	0.1783	0.1626	0.5005
50-60	0.31052	0.14421	0.51008	0.71143	0.58296
	0.6111	0.8170	0.4899	0.2886	0.3023
	5	5	4	4	5
60-70	0.58703	0.11404	1.00000	0.57546	0.80989
	0.4130	0.8551	1.0000	0.6096	0.0966
	4	5	2	3	5
70-80	0.89923	0.10139	.	1.00000	0.91809
	0.1008	0.8711		0.0000	0.0278
	4	5	1	2	5
80-90	0.68925	0.23603	.	.	0.45824
	0.3107	0.7023			0.4377
	4	5	0	0	5
90-100	1.00000	0.14428	.	.	0.99052
	1.0000	0.8169			0.0877
	2	5	0	0	3
100-110	.	0.19539	.	.	.
		0.7528			
	0	5	0	0	0

Parameter codes are shown in Appendix 2.2

Appendix 2.6 (continued)

DEPTH	SOIL PARAMETER #					
(cm)	SI_O	FE_O	AL_O	AL_P	FE_P	AL_E
0-10	0.34953	0.63398	0.49349	0.67888	0.66669	0.48629
	0.5642	0.2507	0.3982	0.2076	0.2191	0.4062
20-30	0.28684	0.55808	0.37588	0.59337	0.36044	0.32065
	0.6399	0.3283	0.5329	0.2915	0.5512	0.5988
30-40	0.26562	0.41605	0.38797	0.43969	0.40002	0.38839
	0.6658	0.4860	0.5187	0.4588	0.5046	0.5182
40-50	0.37565	0.47434	0.23005	0.51597	0.48946	0.50573
	0.5332	0.4195	0.7097	0.3735	0.4027	0.3847
50-60	0.18874	0.37357	0.38031	0.64790	0.54057	0.45260
	0.7611	0.5357	0.5277	0.3521	0.4594	0.5474
	5	5	5	4	4	4
60-70	0.40936	0.46693	0.60398	1.00000	1.00000	1.00000
	0.4937	0.4279	0.2807	1.0000	1.0000	1.0000
	5	5	5	2	2	2
70-80	0.41639	0.44992	0.33455	.	.	.
	0.4856	0.4471	0.5821			
	5	5	5	1	1	1
80-90	0.69881	0.67834	0.42477	.	.	.
	0.1892	0.2081	0.4759			
	5	5	5	0	0	0
90-100	0.59904	0.53649	0.10066	.	.	.
	0.2857	0.3513	0.8721			
	5	5	5	0	0	0

Parameter codes are shown in Appendix 2.2

Appendix 2.6 (continued)

DEPTH	SOIL PARAMETER #					
(cm)	FE_E	TEB	AL_EX	CEC	ECEC	BS_C
0-10	-0.80405	-0.63977	0.53370	0.05435	-0.68323	-0.54183
	0.1010	0.2450	0.3543	0.9308	0.2035	0.3455
20-30	-0.70571	0.08969	-0.34553	0.38713	-0.38725	0.17372
	0.1830	0.8860	0.5690	0.5197	0.5196	0.7799
30-40	0.05730	0.08061	-0.34230	0.54267	-0.27462	0.00452
	0.9271	0.8975	0.5728	0.3446	0.6548	0.9942
40-50	-0.04391	-0.13915	-0.22102	0.52550	-0.31472	-0.14921
	0.9441	0.8234	0.7209	0.3631	0.6060	0.8107
50-60	-0.03601	-0.49085	0.57822	0.83392	0.04972	-0.78762
	0.9640	0.5092	0.4218	0.1661	0.9503	0.2124
	4	4	4	4	4	4
60-70	1.00000	1.00000	1.00000	1.00000	1.00000	1.00000
	1.0000	1.0000	1.0000	1.0000	1.0000	1.0000
	2	2	2	2	2	2
70-80	.	.	.	.	.	.
	1	1	1	1	1	1

Parameter codes are shown in Appendix 2.2

Appendix 2.6 (continued)

DEPTH	SOIL PARAMETER #					
(cm)	BS_E	CA	MG	K	NA	H
10	-0.54667	-0.63985	-0.39395	-0.19440	0.29567	-0.52438
	0.3404	0.2449	0.5117	0.7541	0.6291	0.3643
20-30	0.13853	0.06273	0.02506	0.22599	0.44398	-0.13459
	0.8242	0.9202	0.9681	0.7147	0.4539	0.8291
30-40	0.16267	0.09928	-0.05390	0.02131	0.22915	-0.35503
	0.7938	0.8738	0.9314	0.9729	0.7108	0.5576
40-50	-0.05547	-0.05365	-0.16620	-0.07672	0.50405	0.00000
	0.9294	0.9317	0.7894	0.9024	0.3865	1.0000
50-60	-0.86124	-0.46441	-0.63354	0.50966	-0.23231	-0.50592
	0.1388	0.5356	0.3665	0.4903	0.7677	0.4941
	4	4	4	4	4	4
60-70	1.00000	1.00000	1.00000	1.00000	1.00000	1.00000
	1.0000	1.0000	1.0000	1.0000	1.0000	1.0000
	2	2	2	2	2	2
70-80	.	.	.	.	.	.
	1	1	1	1	1	1

Parameter codes are shown in Appendix 2.2

APPENDIX 2.7 : CORRELATION COEFFICIENTS OF MATAGOURI AERIAL VOLUME AND SOIL CHEMICAL PARAMETERS BETWEEN 0 - 100 CM DEPTH ON T1-T4

Correlation Coefficient (r) ;
Significance probability ;
sample number (n=5 unless otherwise shown)

DEPTH	SOIL PARAMETER #					
(cm)	PH	PHCL	P_XRF	P_TOT	P_AP	P_OR
0-10	0.81693	0.72270	-0.53510	-0.70083	-0.75663	-0.66111
	0.0914	0.1678	0.3528	0.1874	0.1387	0.2244
20-30	0.60903	0.45282	-0.63298	-0.66446	-0.49534	-0.70377
	0.2756	0.4438	0.2517	0.2212	0.3961	0.1847
30-40	0.74751	0.33585	-0.60820	-0.62063	-0.18906	-0.68365
	0.1464	0.5806	0.2764	0.2640	0.7607	0.2032
40-50	0.97788	0.60462	-0.44598	-0.40509	0.05132	-0.54828
	0.0039	0.2801	0.4516	0.4987	0.9347	0.3387
50-60	0.91542	0.89547	-0.42276	-0.38804	-0.11431	-0.56340
	0.0292	0.0399	0.4782	0.5186	0.8548	0.3227
60-70	0.80998	0.90691	-0.29426	-0.33161	-0.31823	-0.17290
	0.0965	0.0336	0.6308	0.5857	0.6018	0.7810
70-80	0.87101	0.85618	-0.25280	-0.32081	-0.62501	0.46669
	0.0545	0.0640	0.6816	0.5987	0.2596	0.4281
80-90	0.87097	0.75673	-0.25727	-0.33496	-0.72414	0.38177
	0.0546	0.1387	0.6761	0.5816	0.1665	0.5260
90-100	0.90485	0.79686	-0.99741	-0.92574	-0.95895	-0.10712
	0.0347	0.1065	0.0459	0.0743	0.0411	0.8929
	5	5	3	4	4	4
100-110	0.9069	0.80143	-0.23811	.	.	.
	0.0336	0.1030	0.6997			
	5	5	5	1	1	1

Parameter codes are shown in Appendix 2.2

Appendix 2.7 (continued)

DEPTH	SOIL PARAMETER #				
(cm)	P_RET	NaF	N	C	LOI
0-10	-0.91222	-0.59567	-0.73390	-0.88138	-0.70399
	0.0308	0.2892	0.1580	0.0482	0.1845
	4	5	4	4	5
20-30	-0.96359	-0.58115	-0.78008	-0.90528	-0.98449
	0.0083	0.3041	0.1196	0.0345	0.0023
	4	5	4	4	5
30-40	-0.96684	-0.90838	-0.75571	-0.81746	-0.92151
	0.0072	0.0328	0.1395	0.0910	0.0261
	4	5	4	4	5
40-50	-0.94145	-0.88913	-0.68311	-0.81227	-0.81059
	0.0169	0.0436	0.2037	0.0948	0.0961
	4	5	4	4	5
50-60	-0.95508	-0.91393	-0.71605	-0.86773	-0.83410
	0.0114	0.0299	0.2840	0.1323	0.0791
	5	5	4	4	5
60-70	-0.37831	-0.89811	1.00000	0.50000	-0.19611
	0.6217	0.0384	0.0000	0.6667	0.7519
	4	5	2	3	5
70-80	-0.49675	-0.85154	.	.	-0.03682
	0.5033	0.0671	0.9531		
	4	5	1	2	5
80-90	-0.14539	-0.83447	.	.	0.28149
	0.8546	0.0788	0.6464		
	4	5	0	0	5
90-100	1.00000	-0.87418	.	.	-0.29193
	0.0000	0.0526	0.8114		
	2	5	0	0	3
100-110	.	-0.86927	.	.	.
		0.0556			
	0	5	0	0	0

Parameter codes are shown in Appendix 2.2

Appendix 2.7 (continued)

DEPTH	SOIL PARAMETER #					
(cm)	SI_O	FE_O	AL_O	AL_P	FE_P	AL_E
0-10	0.32031	-0.87724	-0.96028	-0.89645	-0.90004	-0.98027
	0.5993	0.0507	0.0094	0.0394	0.0374	0.0033
20-30	-0.29729	-0.89229	-0.96418	-0.94740	-0.95483	-0.97498
	0.6271	0.0417	0.0081	0.0144	0.0114	0.0047
30-40	-0.60913	-0.92564	-0.98629	-0.93705	-0.97966	-0.90458
	0.2755	0.0241	0.0019	0.0188	0.0035	0.0349
40-50	-0.57110	-0.78355	-0.88624	-0.94647	-0.93499	-0.96355
	0.3146	0.1169	0.0453	0.0147	0.0197	0.0083
50-60	-0.77990	-0.96364	-0.34443	-0.92884	-0.43623	-0.67612
	0.1198	0.0083	0.5703	0.0712	0.5638	0.3239
	5	5	5	4	4	4
60-70	-0.94984	-0.91075	-0.12207	1.00000	1.00000	1.00000
	0.0134	0.0316	0.8450	0.0000	0.0000	0.0000
	5	5	5	2	2	2
70-80	-0.94413	-0.95381	0.51945	.	.	.
	0.0157	0.0118	0.3697			
	5	5	5	1	1	1
80-90	-0.80674	-0.71487	0.37509	.	.	.
	0.0990	0.1747	0.5339			
	5	5	5	0	0	0
90-100	-0.93785	-0.88953	0.68660	.	.	.
	0.0184	0.0433	0.2004			
	5	5	5	0	0	0

Parameter codes are shown in Appendix 2.2

Appendix 2.7 (continued)

DEPTH	SOIL PARAMETER #					
(cm)	FE_E	TEB	AL_EX	CEC	ECEC	BS_C
0-10	0.06270	0.42801	-0.52876	-0.88987	0.31676	0.83876
	0.9202	0.4722	0.3596	0.0431	0.6035	0.0758
10-20	-0.15516	0.70492	-0.28992	-0.90795	0.58679	0.66559
	0.8032	0.1837	0.6361	0.0331	0.2983	0.2201
20-30	-0.29407	0.78135	-0.16842	-0.72282	0.81979	0.83047
	0.6311	0.1186	0.7866	0.1677	0.0893	0.0816
30-40	-0.07097	0.82003	-0.37674	-0.89544	0.82080	0.84896
	0.9097	0.0891	0.5319	0.0399	0.0886	0.0688
40-50	-0.52233	-0.28427	-0.34592	-0.65104	-0.34891	-0.01262
	0.4777	0.7157	0.6541	0.3490	0.6511	0.9874
	4	4	4	4	4	4
50-60	1.00000	1.00000	1.00000	1.00000	1.00000	1.00000
	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000
	2	2	2	2	2	2
60-70	.	.	.	.	.	.
	1	1	1	1	1	1

Parameter codes are shown in Appendix 2.2

Appendix 2.7 (continued)

DEPTH	SOIL PARAMETER #					
(cm)	BS_E	CA	MG	K	NA	H
0-10	0.53327	0.63587	-0.20689	-0.65040	-0.11787	-0.44718
	0.3547	0.2489	0.7385	0.2347	0.8503	0.4502
20-30	0.63329	0.68988	0.76750	0.62742	0.04067	-0.71281
	0.2514	0.1974	0.1298	0.2572	0.9482	0.1766
30-40	0.68055	0.76040	0.88826	0.67508	0.21907	0.07135
	0.2060	0.1356	0.0441	0.2112	0.7233	0.9092
40-50	0.74363	0.82107	0.89108	0.81759	0.23536	-0.60851
	0.1497	0.0884	0.0424	0.0909	0.7031	0.2761
50-60	0.01459	-0.36464	0.25476	0.03292	0.67526	0.39469
	0.9854	0.6354	0.7452	0.9671	0.3247	0.6053
	4	4	4	4	4	4
60-70	1.00000	1.00000	1.00000	1.00000	1.00000	1.00000
	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000
	2	2	2	2	2	2
70-80	.	.	.	.	.	.
	1	1	1	1	1	1

Parameter codes are shown in Appendix 2.2

APPENDIX 6.1 : SAMPLE DRYING

To check that relatively large (up to *ca* 400 g) herbage samples were properly dried when bagged and closely packed in the oven, three representative lotus bags (mean wt. 350 g) were periodically weighed throughout drying. The resulting drying curve (Fig. 1) showed that the standard 24 hour drying treatment was ample for complete drying.

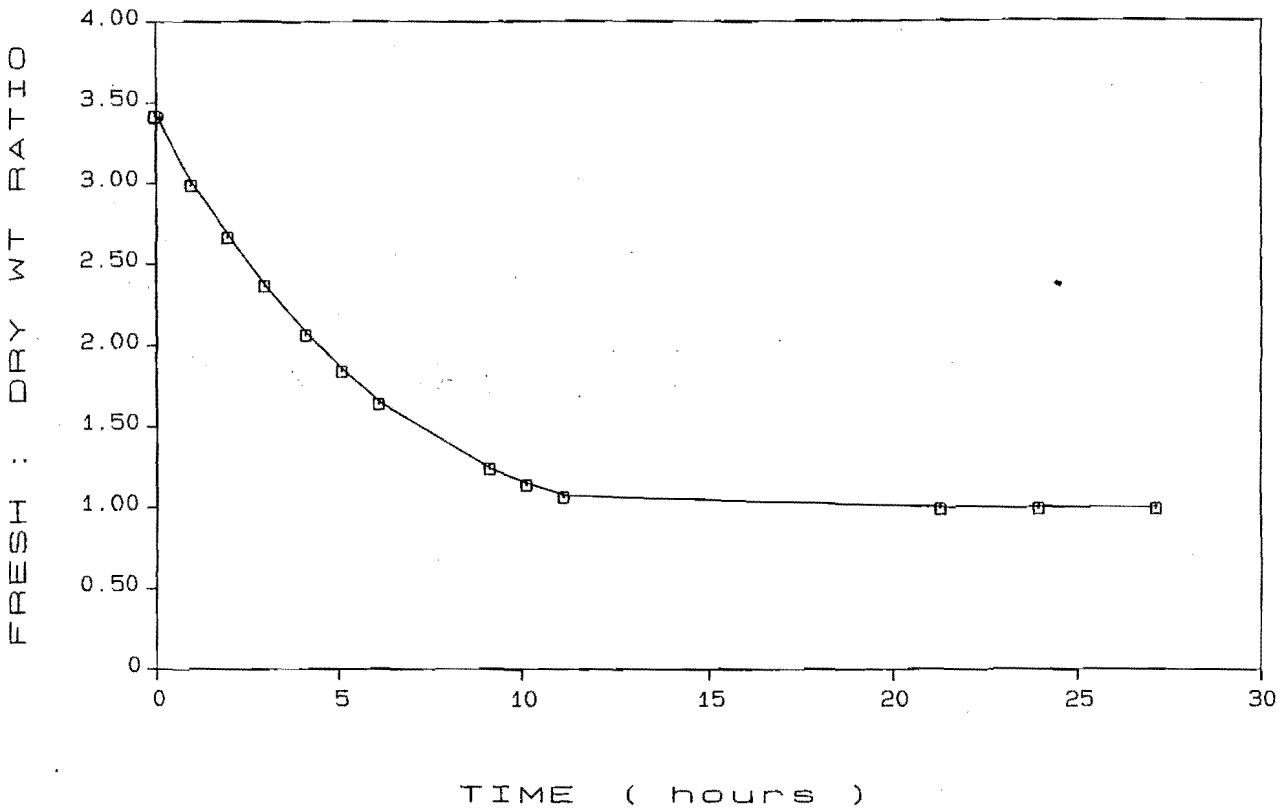

Figure 1 : Drying curve for lotus herbage samples at 80 ^{0}C.

APPENDIX 6.2 : CHEMICAL ANALYSES

Nitrogen and Phosphorus were determined using a Pye Unicam AC6 automatic chemistry unit and SP6 spectrophotometer (Pye Unicam 1971, 1980).

(a) Wet Acid Digestion

Samples were re-dried overnight at 50- 55 °C, cooled in a desiccator and approximately 0.2500 (± 0.0008) g weighed in a paper pan. Sample and pan were positioned at the bottom of a 30 x 2.5 cm constricted neck reflux tube and approximately 1 g of selenium: K_2SO_4 powder (1:100) added as a catalyst. Five ml of concentrated sulphuric acid (AR grade) was then added. Eighteen samples, each duplicated, plus two standard samples (either lotus or clover bulked across all treatments) and two reagent blanks were digested in a 40 tube digestor for 1 hour at 240 °C, then 3 hours at 390 °C. After digestion, digests were cooled and then mixed while they were being made up to 100 ml with distilled water. A 20 ml aliquot was decanted off and stored in a glass vial until analysis.

(b) Phosphorus

P concentration in the digestate was determined colorimetrically by the phosphovanadomolybdate method (Kitson and Mellon 1944; Parks and Dunn 1963) using standard procedures for discrete sample analysis as specified below. Each digestate was assayed in duplicate and an internal standard inserted in duplicate after every eight assays. A Hewlett-Packard 85 microcomputer programme was used to correct for any baseline drift. A full standard set was repeated approximately every 100 assays to check any drift in slope of the equation calibration.

The analysis method, adapted from Parks and Dunn (1963),was followeed exactly as specified by Pye Unicam (unpublished user notes).

i) Reagents:

Vanadomolybdate solution: 5.00 g of ammonium meta-vanadale (Analar) was dissolved in 500 ml deionized water and 625 m of 69.71% Perchloric acid (AR) added. 100.00 g ammonium molybdate (Analar) was dissolved in 500 ml of deionized water. The two solutions were mixed and made up to 5000 ml volume.

ii) Standards:

Stock solution: 0.4394 g potassium dihydrogen phosphate (AR) dissolved in deionized water and made up to 1 litre.

Working standards: 0, 10, 20, 30, 40, and 50 ml stock solution were pipetted with 10 ml conc. sulphuric acid (AR) into 200 ml volumetric flasks, giving a set of 0-25 ppm standards.

iii) Automatic chemistry unit settings:

Reagent	Position	Syringe (ul)	Sol^{n} volume (ul)
(0) Sample	47	450	20.0
(1) Vanadomolybdate	47	2000	17.2
(2) Deionized water	40	2000	12.0

iv) Spectrophometer settings:

Wave length - 420 nm; Photocell - blue; Mode - concentration; Backoff - 0; Flow Cell - 10 mm; Cycle time - 15 seconds.

v) Calibration and P determination:

After zeroing the spectrophotometer with 10 zero ppm standards, a standard set 0, 5, 10, 15, 25 ppm, assayed in duplicate, was used by a Hewlett-Packard 85 microcomputer to calculate an absorbance:ppm P regression equation. Sample absorbances were converted into ppm P using this equation, then multiplied by a drift corection factor as follows:

$$\text{ppmP in solution} = \text{ppmP} \times \frac{\text{absorbance expected for internal std.}}{\text{absorbance observed from internal std.}}$$

where the expected absorbance was that calculated from the regression for the internal standard being used (usually 5 ppm) and the observed absorbance was the averaged absorbance from a duplicate assay of the internal standard run after every eight assays.

The four assays before each pair of standard and the four after were scaled using the correction factor derived from that pair. Results were converted to mg P/g dry weight.

(c) Nitrogen

Digest N concentration was determined by the indo-phenol blue method (Searle 1984) using standard procedures Pye Unicam (unpublished user notes). Digests were processed similarly to P digests.

i) Reagents:

40.0 gm phenol (AR) was dissolved in 900 ml deionized water and made up to 1 litre volume. 75.0 mg sodium nitroprusside was similarly made up to 1 litre. 50.0 g sodium hydroxide was dissolved in deionized water and 25 ml of commercial bleach (hypochlorite) added and made up to 200 ml volume

ii) Standards:

2.358 g dried ammonium sulphate (AR) was dissolved in deionized water and made to 500 ml volume. Working standards, ranging from 0 to 100 ppm, were prepared in a similar manner as for P.

iii) Automatic chemistry unit settings:

Reagent	Position	Syringe (ul)	Volume (ul)
(0) Sample	47	25	15
(1) Phenol	47	2000	1000
(2) Sodium nitroprusside	40	2000	1000
(3) Alkaline hypochlorite	36	1000	400

iv) Spectrophotometer settings:

Wave length - 550 nm; Photo cell - blue; Mode - concentration; Backoff - 0; Flow cell - 10 mm; Cycle time - 15 seconds.

v) Calibration and N determination:

The procedure was identical with that used for P excepting the different range of standards.

(d) Accuracy of Measurement

To test the accuracy of N and P measurement, inorganic samples of known composition were analysed identically to herbage samples. Three runs of Analar Glycine and one run of Analar Potassium di hydrogen orthophosphate (n = 71 and 16

respectively) were assayed during sample analysis. The samples were selected to give a final concentration range from 10 to 100 ug l of each element in the assay solution.

Results were as follows:

	Observed	Expected	% of Expected
Phosphorus	58.17	57.69	100.8
Nitrogen	186.32	186.56	99.9

There was a close relationship between observed and expected elemental concentrations, at all sample weights, for both elements (for P, $R^2 = 0.996$; for N, $R^2 = 0.981$). The relationship is shown for P in Fig. 1

The results show N and P assessment methods used in this study gave excellent recovery of both N and P.

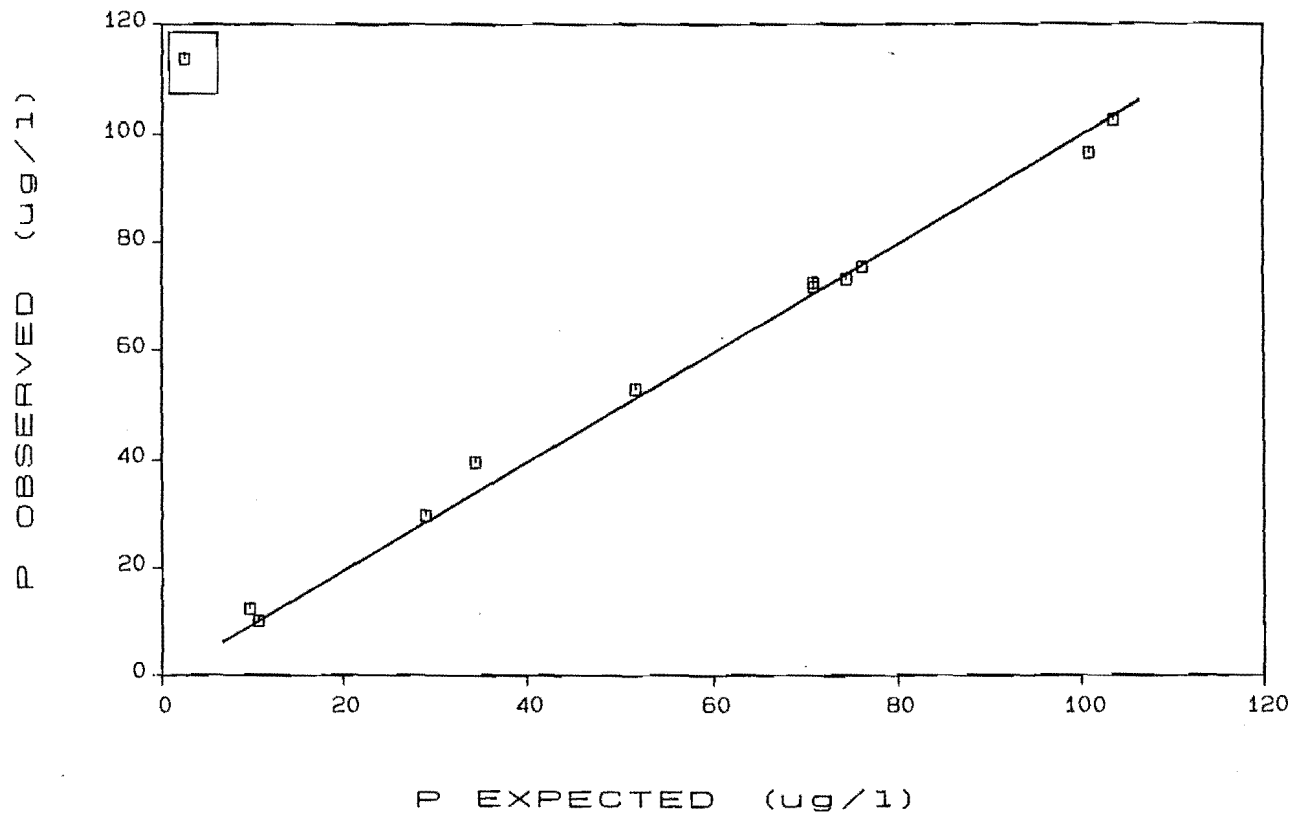

Figure 1 : Observed vs Theoretically Expected P in assay solution.